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COMPARATIVE PHYSIOLOGICAL ECOLOGY OF ARCTIC AND ALPINE POPULATIONS OF *OXYRIA DIGYNA*

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INTRODUCTION

Tundra environments provide extremely severe conditions for plant growth. They are characterized by a short cold growing season of two to three months and a long bitter winter. In North America, such environments occur from the northernmost parts of Greenland, Canada, and Alaska along the mountain crests as far south as Mexico. Gradients of latitude and elevation throughout this extensive range create significant environmental differences between the arctic tundra of the north and the alpine tundra of the south. Length of photoperiod, amount of ultraviolet radiation received, wind force, and magnitude of diurnal temperature fluctuations are outstanding dissimilarities between the superficially similar environments. Bliss (1956) has called attention to these

differences, and many others of a lesser magnitude, in his comparison of microenvironments and plant development in arctic and alpine tundras.

In spite of these environmental gradients, certain arctic-alpine plant species are widely distributed throughout the tundra regions of the northern hemisphere. These plants are low elevation-circumpolar in the north and high elevation-alpine in the great mountain systems of temperate North America and Eurasia.

The question arises, "How are arctic-alpine species able to grow in such diverse environments?" Are they so ecologically plastic that any given member of each population would be able to tolerate all of the possible environmental combinations presented by arctic and alpine habitats? Or, are these species composed of ecological races or ecoclines, each adapted to different aspects of the tundra environment?

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Either solution is theoretically possible, as is a combination of both. Up to now, there has not been enough available evidence to answer either question. However, the results of Turesson (1930) and Clausen, Keck & Hiesey (1948) with wide-ranging species in more temperate environments would tend to favor the second solution.

In an attempt to answer such questions, the environmental requirements of a series of arctic and alpine populations of a selected species, *Oxyria digyna* ("alpine sorrel"), were investigated. The

primary emphasis was on possible morphological and physiological differences between these populations under the impacts of different environments. Of particular importance was the study of those physiological characteristics which might be of adaptive significance. Such an approach should be able to determine if the environmental differences between arctic and alpine habitats are reflected, through natural selection, on the physiological responses of the principal biotypes in the local populations of the species.

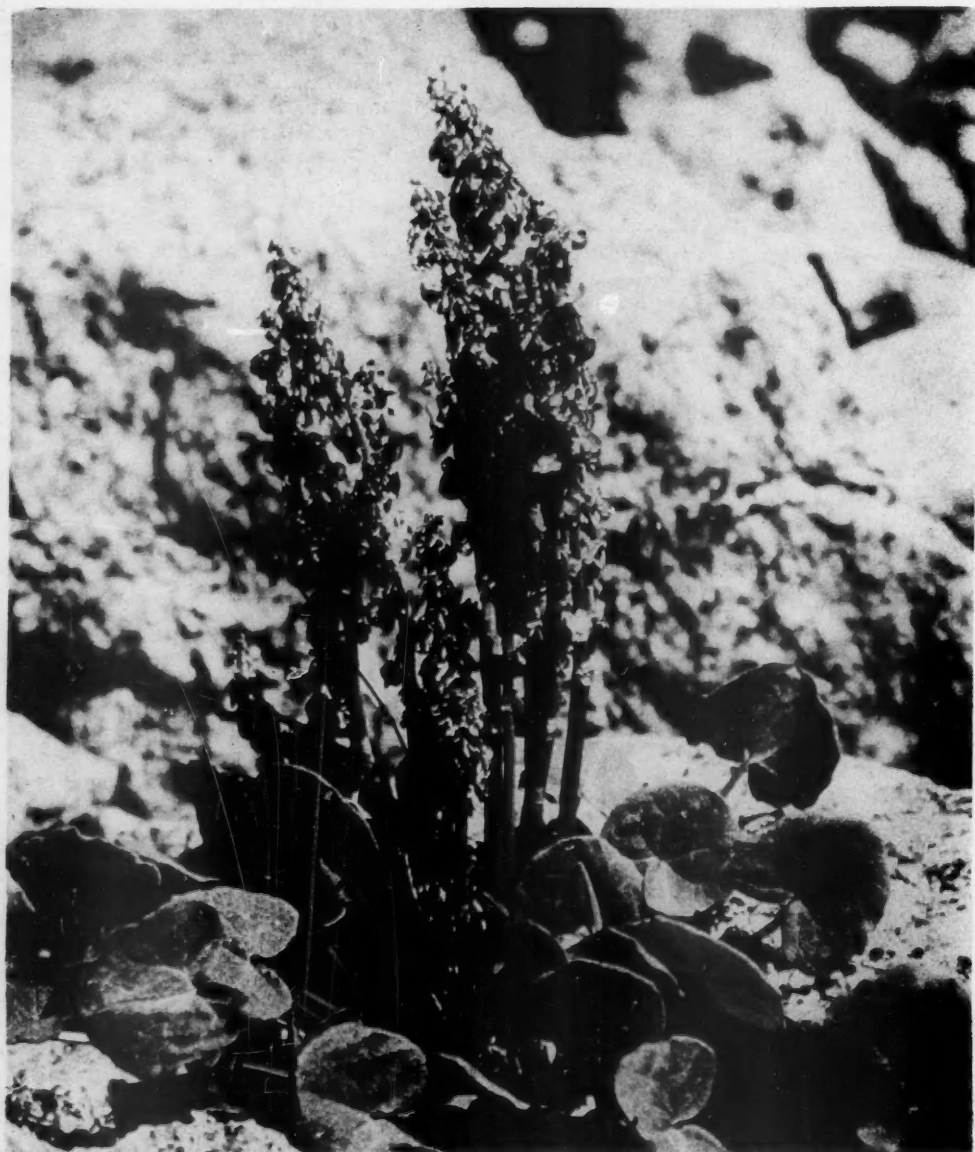


FIG. 1. *Oxyria digyna* in rocky talus at an elevation of 10,200 ft, Beartooth Mountains, Wyoming.

Oxyria digyna (L.) Hill (Fig. 1), a perennial, herbaceous member of the Polygonaceae was selected for this study for several reasons. (1) It has a circumboreal arctic-alpine distribution of wide latitudinal range. It occurs in the arctic tundra as far north as 83° N, and in North America as far south as Arizona in the mountains. (2) A considerable body of information on the physiological processes of this species, in the field, has been assembled (Wager 1938, 1941; Russell 1940b, 1948; Warren Wilson 1954, 1957, 1959, 1960). These studies were almost entirely confined to arctic populations. (3) The seeds of *Oxyria* are easily collected and germinate well. Plants can be grown without difficulty and provide excellent material for physiological investigation. (4) There are few taxonomic difficulties associated with this phylogenetically isolated species. Polunin (1940) has called *Oxyria* one of the few really "good" arctic species, varying from place to place only in size of leaves and height of inflorescences. There is, however, one major difficulty associated with this species. It is not particularly suited for hybridization experiments because of the large numbers of small delicate flowers in the inflorescence. A further complication to such work is the partial apomixis in this species which has been described by Edman (1929).

Utilizing the data of Hultén (1928), the general distribution of *Oxyria* is arctic-alpine circumpolar, with disjunct locations far to the south in the mountains of Europe, Asia, and North America.

The work reported here was financed under a grant from the National Science Foundation (NSF-G3832-Environmental Biology) for which grateful acknowledgment is made. For many courtesies and assistance which made the study possible thanks are due to: Dr. John W. Marr and Dr. William Osburn of the University of Colorado, Dr. Moras L. Shubert of the University of Denver, Dr. S. H. Knight and Dr. Henry L. Northen of the University of Wyoming, Dr. Albert W. Johnson of the University of Alaska, and Dr. A. W. Naylor, Dr. R. L. Barnes, and Miss Pat C. Kerr of Duke University. We are especially indebted to Dr. Edward E. C. Clebsch and Mrs. Barbara Mooney of Duke University whose assistance in both the field and the laboratory was invaluable.

FIELD METHODS

HABITATS DESCRIPTION

During the summer of 1957 and 1958, a latitudinal series of *Oxyria digyna* plants was collected. These arctic and alpine populations were selected to encompass a wide geographic range of tundra habitats. Elevations ranging from sea level to over 12,000 ft and latitudes extending from 38° N to 76° N were included in the population sites. Accessibility of each collection area necessarily determined its exact locale. The locations of these populations in relation to the North American distribution of *Oxyria* are shown in Figure 2.



FIG. 2. North American distribution of *Oxyria digyna* from data of Fernald (1933) and Porsild (1957). Numbers refer to areas from which populations were collected: 1. Elephant's Back, California, 2. Loveland Pass, Colorado, 3. Niwot Ridge, Front Range, Colorado, 4. Medicine Bow Mts., Wyoming, 5. Beartooth Mts., Wyoming, 6. Logan Pass, Montana, 7. Highwood Pass, Alberta, 8. Sunwapta Pass, Alberta, 9. Summit Lake, British Columbia, 10. Donjek Mts., Yukon Territory, 11. Eagle Summit, Alaska, 12. Pitmegea River, Alaska, 13. Sagavanirktok River, Alaska, 14. Pt. Barrow, Alaska, 15. Thule, Greenland, 16. Angel Glacier, Alberta.

The site of the most abundant occurrence of *Oxyria* within each study area was chosen as the local population site. Mass herbarium collections were made and notes on the extent and characteristics of the population were taken. At most sites, the percentage coverage of *Oxyria* and the associated species was quantitatively determined. This was done for a 5 x 5 m square by crossing two diagonal 7.1 m lines within the microsite. The vegetation was sampled by point intercepts at 5 cm intervals along these lines. This made a total of 283 points along the diagonals of the 25 sq m area.

Seeds and/or live plants were collected at each site. The live plants were sent by airmail to North Carolina for greenhouse culture. Soil samples of the upper mineral soil horizons at each location were collected for later analysis.

Unfortunately, uniformly complete information is not available from all the population sites since the collection of seeds or plant material by some contributors was incidental to other tasks in which they were engaged. However, the available data on sites actually visited by at least one or both of the authors make it possible to get some idea of the environment and associates characteristic of *Oxyria* populations in widely scattered parts of its range.

FIELD PHYSIOLOGICAL METHODS

During the summer of 1958, it was possible to carry out a few physiological measurements in the field on two alpine *Oxyria* populations. On one population, Medicine Bow Mts., Wyoming, the carbohydrate content of the leaves and the roots was followed during the course of the growing season. Photosynthesis and respiration rates were measured and leaf chlorophyll content analyzed. On an Alaskan alpine population, Eagle Summit, the carbohydrate content was measured at a single phenological stage and chlorophyll determinations were made.

A Model 29 Liston-Becker Infrared Gas Analyzer (Beckman Instruments, Inc.) was utilized for all photosynthesis and respiration measurements in this study. This model is operated with a six-volt battery, and hence can be used in the field. An Esterline-Angus Model AW direct current milliammeter was used as the recording device.

An open system, as described by Billings, Clebsch & Mooney (1960b), was used for field photosynthesis and respiration measurements. The method consisted of making alternate measurements of the CO_2 content of a gas stream passing over a plant enclosed in a plexiglass chamber and of a "free" air stream. Calculations of the photosynthetic and respiration rates were based on the difference between the CO_2 contents of the two streams with the gas flow rate maintained at 80.6 l/hr.

The plant stream was measured for 15-minute periods, alternating with 5-minute periods for measurement of the air stream.

The analyzer was calibrated prior to each test period by flushing the calibration system free of CO_2 by use of an absorbent (Ascarite) in the air stream. Then, definite aliquots of pure CO_2 were injected into the closed calibration system by means of a hypodermic needle. A calibration curve was constructed to indicate mg CO_2 /l.

Petioles of 8 to 10 *Oxyria* leaves (attached to a single rooted plant) were inserted through a slotted plexiglass base plate and sealed in place with Apiezon "Q" type sealing compound. A one liter plexiglass photosynthetic chamber was then sealed on top of the base plate, thus completely enclosing the leaves. During the course of a test period a continuous record of the radiation received was recorded with an Instruments Corporation Recording Pyrheliometer. The temperature was measured at 5-minute intervals inside and outside of the photosynthetic chamber using shielded mercury-in-glass thermometers. Light intensity in foot candles was read on a photoelectric illumination meter (Weston Electrical Instrument Corp.) at 5-minute intervals.

An attempt to control excessive temperature build-up within the chamber was made by placing a Corning infrared glass filter, CS1-69 no. 4600 M-2040, so that it intercepted the direct solar radiation. Also, snow was packed around the base of the chamber, which not only helped in temperature control but pre-

vented moisture condensation on the upper chamber surface.

Two test runs were completed on *Oxyria*, the first, of 1 hr duration on leaves of a plant in early flower bud stage on July 9, and another of 2 hrs duration on a plant in late flower bud stage on July 22. At the conclusion of each run, the chamber was covered with a black cloth for a ten minute period for determinations of dark respiration.

From the millimeter recordings, calculations of the photosynthetic rate of 1.5 minute intervals were made and expressed on three bases: per gm of fresh weight per hr, per sq dm of leaf surface (twice the area of the leaf) per hr, and per milligram of total chlorophyll per hr.

The procedure used for carbohydrate extraction and analysis has been previously described (Mooney & Billings 1960) and is comparable to the procedures of Russell (1940b) and Warren Wilson (1954). Samples of the upper tap root and leaves were taken at definite phenological stages and analyzed in triplicate for starch and total sugar, the sum of which was considered "total carbohydrate."

Determinations were made of the total nitrogen content of the alcohol-insoluble residues by the method of Block & Bolling (1951) on all the samples taken for carbohydrate analysis.

Samples of *Oxyria* leaves were collected from the Medicine Bow Mts., Wyoming, and Eagle Summit, Alaska, for chlorophyll determinations. The fresh weight of the sample was taken, the leaf outline traced, and the sample placed in a green vial containing 80% acetone. These were used later for determination of chlorophyll content by the spectrophotometric method of Arnon (1949).

LABORATORY METHODS

All plants used in laboratory experimental work were grown from field-collected seed. The plants were grown in a standard greenhouse soil mixture (two parts loam, one part leaf mold, and one part sand) in 4-inch clay pots. These plants were maintained either in the greenhouse or in especially constructed growth chambers, watered daily, and fertilized with a "complete" liquid fertilizer at regular intervals.

GROWTH CHAMBER DESIGN

Plants utilized for laboratory physiological measurements and for detailed analysis of growth and phenological development were grown in controlled-environment growth chambers. These low-temperature growth chambers constructed from "island-type" display freezer units have been described by Billings, Clebsch & Mooney (1960a). It was possible to control and cycle both temperature and light periods in the chambers enabling a simulation of temperature and light cycles in natural tundra environments.

CHAMBER PROGRAMMING

Three growth chambers were utilized for experimentation. One chamber was used to simulate the

diurnal cycle of an alpine environment at a latitude of approximately 41° N. The day temperature was controlled at 65° F for a 12-hr period and the night temperature at 40° F for an equal time. A 15-hr photoperiod was maintained. These values were selected to represent average alpine mid-summer conditions in the Medicine Bow Mts., Wyoming, as measured by Bliss (1956). This simulation of the environment involved control of only thermoperiod and photoperiod.

A second chamber simulated growing season conditions of the Alaskan Arctic Coastal Plain at 71° N. The day temperature was kept at 55° F and the night at 35° F, both for alternating 12-hr thermoperiods. This chamber was constantly lighted.

The two chambers described above will be referred to as the "alpine" and "arctic" chambers, respectively, throughout the text.

A third chamber was used first at a constant 50° F temperature and 12-hr photoperiod. Later, the same temperature was maintained but the photoperiod was changed to 17 hrs. This will be referred to as the "constant temperature" chamber.

CHAMBER UTILIZATION

Two separate sets of plants were placed consecutively in the chambers during the duration of the project. Each set consisted of either 4 or 5 different populations, usually 10 plants to the population, in each of the 3 chambers. At weekly intervals, each plant was scored for phenological development and the inflorescences of fruiting specimens were harvested and pressed. In addition to recording phenological development, growth measurements were made at regular periods on one set of populations.

Almost all plants utilized in the laboratory for physiological measurements were taken directly from chambers for use. Exceptions to this procedure will be noted in the text.

PHOTOSYNTHESIS AND RESPIRATION MEASUREMENTS

For the laboratory, a "closed" system was designed for use with the infrared gas analyzer. It was not possible to utilize the "open" system that was employed in the field because of the rapidly fluctuating CO_2 content of the semi-urban air. A plant was placed in a closed system of known CO_2 concentration and the time was measured for a given amount of CO_2 to be added to or removed from this system. In actual practice, the operating range was .0285 to .0315% CO_2 in the air stream.

In the laboratory, it was possible to control the temperature of the air within the photosynthetic chamber. A thermistor inside the chamber was utilized as the sensing element for a Yellow Springs Instrument Model 71 Temperature Controller. The controller was attached to an ice-water compressor thus maintaining the water at any pre-set temperature. The water from the cooler was circulated around the photosynthetic chamber by use of a water pump.

Four 300-watt incandescent "sealed beam" spot lights were used for both a light and a heat source in the system. Illumination at the base of the photosynthetic chamber could be maintained from 0 to 7,000 fc by use of switches and a rheostat.

The standard air flow rate used in all laboratory gas exchange measurements was approximately 170 l (6 cu ft) per hr.

DESCRIPTIONS OF ARCTIC AND ALPINE OXYRIA HABITATS

The similarities and differences of the principal Oxyria habitats investigated throughout a wide range of latitudes are presented in the following section. The location, elevation, exposure, parent material, some of the soil characteristics, and associated species are given for these Oxyria microsites.

GENERAL HABITAT DESCRIPTIONS

Elephant's Back, California. The only Oxyria population collected from the Sierra Nevada was located in Alpine County, California, south of Carson Pass ($38^{\circ} 42' \text{ N}$, $119^{\circ} 57' \text{ W}$). Collections were made at this site on August 15, 1957. Oxyria plants were growing on the very steep northeast-facing talus of Elephant's Back at an elevation of 9,100 ft. The talus, which is composed of volcanic andesitic breccia, is a site of very late snowmelt. The microsite is scantily vegetated with Oxyria as well as *Agropyron pringlei* (Scribn. & Sm.) Hitchc., *Arabis lemmonii* Wats., *Arenaria nuttallii* Pax., *Lupinus lyallii* Gray, *Penstemon heterodoxus* Gray, *Phacelia frigida* Greene, *Ranunculus eschscholtzii* Schlecht. var. *oxynotus* (Gray) Jeps., *Senecio fremontii* T. & G. var. *occidentalis* Gray, and *Calyptidium umbellatum* (Torr.) Greene.

Loveland Pass, Colorado. This population was collected at an elevation of 12,300 ft in the Loveland Pass area of Colorado ($39^{\circ} 40' \text{ N}$, $105^{\circ} 53' \text{ W}$). The microsite is situated on a northwest-sloping (25°) granitic boulder field. Oxyria is restricted to rock crevice areas within the boulder field, although in the general area it is also found on gravelly, otherwise unvegetated areas, such as road fills and drainage ditches. Associated with Oxyria in the soil pockets are *Geum turbinatum* Rydb., *Primula angustifolia* Torr., *Saxifraga rhomboidea* Greene, *Trisetum spicatum* (L.) Richt., and *Selaginella densa* Rydb.

Oxyria was in bloom at the time of collection, and some of the flowers were smutted. These were the only smutted individuals noted in all of the field collections.

Pikas (*Ochotona princeps*), small alpine mammals, were very evident in the site area on the August 5, 1957, collection date.

Niwot Ridge, Front Range, Colorado. The Niwot Ridge population was collected in the vicinity of the University of Colorado Institute of Arctic and Alpine Research Tundra Laboratory on Niwot Ridge in the Front Range of Colorado ($40^{\circ} 04' \text{ N}$, $105^{\circ} 38' \text{ W}$) at an approximate elevation of 12,000 ft. The micro-

site is located on a north-facing stabilized talus (granite and schist) which has a slope of 25°. *Oxyria* is restricted to protected crevices within the talus. Abundant *Oxyria* seedlings were observed on the August 11, 1957, collection date, at which time the mature plants were in flower.

In the protected crevices, *Mertensia viridis* A. Nels. and *Senecio fremontii* T. & G. are prominent. In the more open crevice areas, *Sedum rosea* (L.) Scop., *Cirsium hookerianum* Nutt., *Claytonia megarrhiza* (Gray) Parry, *Trifolium nanum* Torr., *Geum turbinatum* Rydb., and *Trisetum spicatum* (L.) Richt. occur.

Medicine Bow Mountains, Wyoming. The *Oxyria* population selected from this area is located in the crevices of an essentially level quartzite boulder field. The plants are restricted to soil pockets which are formed, in part, through the intense activity of pikas. The microsite is situated at an elevation of 10,800 ft in the northern Libby Flat area of the Medicine Bow Mts. (41° 20' N, 106° 19' W). *Oxyria* also occurs in the Medicine Bow alpine area on rocky north-facing slopes but is not common.

Associated with *Oxyria* within the boulder field are *Aquilegia caerulea* James, *Ribes montigenum* McClatchie, *Senecio fremontii* T. & G., and *Cystopteris fragilis* (L.) Bernh.

Observations and physiological measurements were made on this population throughout the 1958 growing season.

Beartooth Mountains, Wyoming. This population is located on the Beartooth Plateau area approximately 4 mi north of Beartooth Pass (44° 59' N, 109° 25' W) at an elevation of 10,600 ft. The microsite is located on a gentle north-facing portion of the Wyoming Creek drainage. The area is composed of stream-deposited rock fragments, primarily gneiss, ranging from 2 ft in diameter down to gravel size. In spite of the considerable amount of soil surrounding and underlying the rock, the microsite area is essentially vegetationless with the exception of widely scattered clumps of completely exposed *Oxyria* and *Deschampsia caespitosa* (L.) Beauv. This relative lack of vegetation is due to normally late snowmelt.

Oxyria was setting and dispersing fruit on the August 25, 1957, collection date. Even at this date, however, it was apparent that the population area had not been snow-free for long.

Logan Pass, Montana. Seed, only, were collected from an *Oxyria* population growing in the immediate vicinity of Logan Pass, Lewis Range (48° 42' N, 113° 43' W), at an elevation of 6,650 ft. The plants were growing completely exposed on a level sedimentary rock substrate. The collection date was August 27, 1957.

Highwood Pass, Alberta. An *Oxyria* population was selected in the Elk Mountains of Alberta, in the vicinity of Highwood Pass (50° 35' N, 115° 02' W). The plants are found locally abundant in a cirque of 8,000 ft elevation at the base of a fossiliferous limestone talus slide. These plants are growing exposed,

on an east-facing slope (13°) associated with small rocks, but not in crevices. The thin turf is underlain with broken rock. *Oxyria* ranged from full flower to fruiting stage at the time of collection, July 28, 1958.

The results of the vegetational analysis here are given in Table 1. *Oxyria* covers less than 3% of the ground surface, while bare rock has a coverage of over 50%.

Sunwapta Pass, Alberta. *Oxyria* occurs at the base of a stone-stripe area 1 mi southeast of Sunwapta Pass, Alberta (52° 12' N, 117° 08' W). The microsite is located on an east spur of Mt. Athabasca between Hilda Creek and Saskatchewan Glacier at an elevation of 7,200 ft. This late snowmelt habitat is situated on a gentle north-facing slope. Associated with *Oxyria* are *Silene acaulis* L., *Trisetum spicatum* (L.) Richt., and *Poa alpina* L. Plant cover was less than 1% of the ground. Collections of seed and live plants were made here on August 16, 1958.

Summit Lake, British Columbia. A small colony of *Oxyria* was found in this area at the base of a large dolomitic rock outcrop and talus. The north-facing slide area (25° slope) is located at an elevation of 5,300 ft near Summit Lake (58° 37' N, 124° 41' W). *Oxyria* is frequent within the microsite area but is limited to the shallow soil pockets in the slide. Even at the relatively early collection date on August 2, 1958, virtually all of the *Oxyria* fruits had been dispersed.

The percentage cover of the vegetational components is given in Table 1. There is a high percentage of rock cover. Coverage of the site by *Oxyria* is about 2%. The high percentage of moss cover in the general area is reflected in the figures given for this quadrat.

Donjek Mountains, Yukon Territory. The population site selected in the Donjek Mts. (61° 23' N, 139° 27' W) is located on a north-facing solifluction lobe at an elevation of 5,700 ft. The microsite is situated on a 29° slope of the actively flowing lobe where approximately 2 in. of turf overlies a sandy subsoil.

Oxyria is scattered in small clumps throughout the microsite. It is also found in the general area associated with *Salix* and *Cassiope* along rocky stream-sides down to an elevation of less than 4,400 ft.

Because of the late date of collection at the population area on August 25, 1958, several plant identifications in the quadrat sample could not be carried below generic level. All of the species were in late fruit or had dispersed seed and were showing fall coloration at this date. The results of the vegetational analysis are in Table 1.

Eagle Summit, Alaska. A population of *Oxyria* was found immediately south of Eagle Pass (65° 28' N, 145° 24' W), on the Steese Highway, Alaska. It is situated on a northwest-facing 32° slope, at an elevation of 3,800 ft. The microsite is a semi-stabilized talus with small gravelly soil pockets. The substrate rock is largely mica-schist.

TABLE 1. Vegetational analyses at Oxyria microsites in the middle and northern parts of its North American range. Figures are percentage cover.

Species	Highwood Pass	Summit Lake	Donjek Mts.	Eagle Summit	Pitmegea River	Saga- vanirktok River	Point Barrow
<i>Achillea lanulosa</i> Nutt.	.36	—	—	—	—	—	—
<i>Anemone parvifolia</i> Michx.	.72	—	—	—	—	—	—
<i>Antennaria alpina</i> (L.) Gaertn.	1.8)	—	—	—	—	—	—
<i>Arnica cordifolia</i> Hook.	.72	—	—	—	—	—	—
<i>Carex haydeniana</i> Olney	2.88	—	—	—	—	—	—
<i>Castilleja occidentalis</i> Torr.	.72	—	—	—	—	—	—
<i>Deschampsia caespitosa</i> (L.) Beauv.	.36	—	—	—	—	—	—
<i>Draba crassifolia</i> R. Grah.	.72	—	—	—	—	—	—
<i>Epilobium alpinum</i> L.	1.08	—	—	—	—	—	—
<i>Erigeron peregrinus</i> (Pursh) Greene subsp. <i>callianthemus</i> (Greene) Cronq.	1.44	—	—	—	—	—	—
<i>Festuca brachyphylla</i> Schultes.	.72	—	—	—	—	—	—
<i>Juncus drummondii</i> E. Meyer	.72	—	—	—	—	—	—
<i>Luzula spicata</i> (L.) DC.	.72	—	—	—	—	—	—
<i>Myosotis alpestris</i> Schmidt.	.36	—	—	—	—	—	—
<i>Oxyria digyna</i> (L.) Hill	2.88	2.11	.71	23.84	31.54	25.80	22.70
<i>Phleum alpinum</i> L.	.36	—	—	—	—	—	—
<i>Poa alpina</i> L.	5.40	5.26	—	—	—	—	—
<i>Poa epilis</i> Scribn.	.72	—	—	—	—	—	—
<i>Potentilla diversifolia</i> Lehm.	.36	—	—	—	—	—	—
<i>Salix arctica</i> Pall. var. <i>araioclada</i> (Schneid.) Raup.	2.88	—	—	—	—	—	—
<i>Salix nivalis</i> Hook.	3.24	—	—	—	—	—	—
<i>Saxifraga lyallii</i> Engler	.36	—	—	—	—	—	—
<i>Sibbaldia procumbens</i> L.	1.44	—	—	—	—	—	—
<i>Taraxacum lyratum</i> (Ledeb.) DC.	.36	—	—	—	—	—	—
<i>Antennaria monocephala</i> DC.	—	.35	.36	—	—	—	—
<i>Draba nivalis</i> Liljebl. var. <i>elongata</i> S. Wats.	—	1.40	—	—	—	—	—
<i>Erigeron humilis</i> Grah.	—	.35	—	—	—	—	—
<i>Poa leptocoma</i> Trin.	—	1.75	—	—	—	2.47	—
<i>Polygonum viviparum</i> L.	—	1.05	.36	—	—	—	—
<i>Salix arctica</i> Pall.	—	8.77	—	—	—	—	—
<i>Saxifraga punctata</i> L.	—	1.40	—	—	1.79	—	.35
<i>Trisetum spicatum</i> (L.) Richt.	—	5.61	—	.71	6.09	3.89	—
<i>Artemisia alaskana</i> Rydb.	—	—	.71	1.78	—	—	—
<i>Carex</i> sp.	—	—	10.71	3.20	—	—	—
<i>Cassiope tetragona</i> (L.) D. Don	—	—	37.50	—	—	—	—
<i>Dryas octopetala</i> L. subsp. <i>punctata</i> (Juz.) Hult.	—	—	.71	—	—	—	—
<i>Oxytropis</i> sp.	—	—	.71	—	—	—	—
<i>Pedicularis</i> sp.	—	—	.36	—	—	—	—
<i>Salix polaris</i> Wahlenb. subsp. <i>pseudopolaris</i> (Flod.) Hult.	—	—	16.79	5.34	—	—	—
<i>Salix reticulata</i> L.	—	—	.36	—	.36	—	—
<i>Silene acaulis</i> L.	—	—	3.57	—	—	—	—
<i>Luzula wahlenbergii</i> Rupr.	—	—	—	2.85	—	—	—
<i>Polemonium boreale</i> Adams	—	—	—	1.07	—	—	—
<i>Aconitum delphinifolium</i> DC. subsp. <i>paradozum</i> (Rechb.) Hult.	—	—	—	—	.36	—	—
<i>Artemisia</i> sp.	—	—	—	—	1.43	—	—
<i>Draba</i> sp.	—	—	—	—	.36	—	—
<i>Epilobium latifolium</i> L.	—	—	—	—	2.15	—	—
<i>Equisetum arvense</i> L.	—	—	—	—	.36	—	—
<i>Luzula nivalis</i> (Laest.) Beurl.	—	—	—	—	2.87	—	—
<i>Poa arctica</i>	—	—	—	—	24.01	—	25.53
<i>Salix phlebophylla</i> Ands.	—	—	—	—	8.24	—	—
<i>Stellaria monantha</i> Hult.	—	—	—	—	2.51	—	—
<i>Carex lachenalii</i> Schk.	—	—	—	—	—	.35	—
<i>Salix rotundifolia</i> Trautv.	—	—	—	—	—	2.12	.72
<i>Saxifraga cernua</i> L.	—	—	—	—	—	.71	.35
<i>Cochlearia officinalis</i> L.	—	—	—	—	—	—	5.32
<i>Ranunculus nivalis</i> L.	—	—	—	—	—	—	10.64
<i>Taraxacum alaskanum</i> Rydb.	—	—	—	—	—	—	1.42
Lichens	.36	—	3.57	2.85	—	6.71	.35
Mosses	5.76	28.42	6.43	8.90	12.90	38.16	22.34
Liverworts	—	1.05	—	—	—	—	—
Total vegetational cover	37.41	57.54	82.86	50.53	94.98	80.21	89.72
Bare soil	8.99	6.67	17.14	—	5.02	19.79	10.28
Rock	53.60	35.79	—	49.47	—	—	—

Oxyria is extremely abundant in the microsite as is shown by the vegetational analysis in Table 1. It comprises almost a fourth of the total cover. However, it appears to be mainly of local occurrence, appearing in rock slides and also along the road cut.

The roots of *Oxyria* here were infested with woolly aphids, the only such infestation noted in the field collections.

The collared pika, *Ochotona collaris*, was very active in the rock slide at the time of collection on August 14, 1958.

Pitmegea River, Alaska. An *Oxyria* population was selected at the mouth of the Pitmegea River on the Arctic Ocean (68° 56' N, 164° 38' W), on the northern coastal plain of Alaska. This site is situated at the base of a north-facing shale bluff with a slope of 24°. The combined talus and solifluction lobe is a site of late snowmelt. *Oxyria* is very abundant in the microsite, constituting over 30% of the cover (Table 1). Collections were made here on August 18, 1958.

Unfortunately, a number of herbarium specimens of the associated plants were lost in transit, hence some of the identifications are to the generic level only.

This station, and the remainder to be discussed, are all arctic tundra sites; those previously discussed have been located along a south to north alpine tundra environmental gradient.

Sagavanirktok River, Alaska. A population of *Oxyria* was chosen in the Franklin Bluffs section of the Sagavanirktok River (69° 50' N, 148° 40' W), on the Arctic Coastal Plain of Alaska. The microsite is located on a terrace with a very gentle (1°) west-facing slope which evidently has late-lying snow. The elevation of this site is under 500 ft.

Oxyria is abundant in the sample, constituting 25% of the cover (Table 1). Mosses, however, comprise an even greater portion of the sample.

In the general area, *Oxyria* is frequently found in late snowmelt areas. Collections were made at this site on August 13, 1958.

Pt. Barrow, Alaska. In the Pt. Barrow region (71° 17' N, 156° 47' W), there are occasional concentrations of *Oxyria* on the eroding surfaces of the dissected sea cliffs. At such microsites where snow accumulates and melting is slow, *Oxyria* may be very abundant although quite dwarfed and with flowering stalks uncommon.

Such a concentration of *Oxyria* was chosen as a collection site on August 21, 1958. The population area is less than 50 ft in elevation and is south-facing with a 25° slope.

Although *Oxyria* is quite abundant in the microsite area, comprising over 20% of the cover (Table 1), it becomes rare at a distance of only a few hundred meters inland.

SOIL ANALYSES

Only limited analyses were carried out on the soil samples collected in the field: percentage of sample greater than 2 mm in diameter, pH, and total nitro-

gen. Total nitrogen was determined by the Kjeldahl method, and pH determinations were made by the method of Metson (1956). The results of the limited soil survey are presented in Table 2 as averages of duplicate determinations.

TABLE 2. Soil analyses for *Oxyria* population areas

Location	Percent over 2 mm diam.*	Percent total N	pH
Loveland Pass.....	38.5	.37	5.30
Niwot Ridge.....	3.7	.30	5.35
Medicine Bow Mts.....	3.4	.43	5.50
Beartooth Mts.....	51.8	.07	5.60
Highwood Pass.....	3.6	.78	7.00
Summit Lake.....	5.0	.32	7.80
Donjek Mts.....	39.0	.20	6.25
Eagle Summit.....	44.0	.11	5.85
Pitmegea River.....	41.0	.21	7.35
Sagavanirktok River.....	40.4	.21	7.75
Pt. Barrow.....	17.5	.29	6.25

* Fraction over 2 mm diameter and total nitrogen are on an air-dry weight basis.

All of the soils from *Oxyria* habitats in the Yukon Territory and Alaska have a high percentage of gravel while those of the southern alpine stations usually have low gravel percentages. Loveland Pass, where the population occurs in crevices of severely weathered granite, and the Beartooth Mts., where the observed population grows on stream-deposited gravels, are the two alpine locations where the soil has a high rock and gravel content.

The total nitrogen values are generally high, which may be related to the high incidence of small mammal activity coincident with *Oxyria* populations. The only low value is from soil of the Beartooth stream gravels. With this exception, the southern alpine soils exhibit higher nitrogen values than those of northern soils.

The pH values range from acidic to basic, demonstrating the broad tolerance of *Oxyria* as a species in regard to reaction of the substrate.

Russell (1940a) presents pH and total nitrogen values for various *Oxyria* habitats on Jan Mayen Island. The pH there ranged from 7.2 to 7.6 and the total nitrogen from 0.10 to 0.17%, values which are in keeping with those given here for arctic stations. However, Warren Wilson (unpublished data) found a wider range in soil nitrogen in *Oxyria* habitats on Jan Mayen, with values extending from 0.008 to 1.091%.

HABITAT SUMMARY

Throughout the range of the present work, the southern and northern alpine areas, and the Alaskan Arctic, habitats of *Oxyria* generally appear to have late snowmelt as a common denominator. *Oxyria* in the south is usually associated with crevices or rock in some form: talus, streamside gravel, boulder field, or shallow fractured rock substrate. As a result of such rocky surfaces, alpine *Oxyria* sites are very

TABLE 3. Analysis of certain morphological characteristics of *Oxyria* populations as exhibited under field, controlled environment, and greenhouse conditions

Location	AVERAGE LEAF LENGTH/LEAF WIDTH RATIO						AVERAGE INFLORESCENCE BRANCH NUMBER			
	Field		Chambers		Greenhouse		Field		Chambers	
	N	Ratio	N	Ratio	N	Ratio	N	Branch number	N	Branch number
Elephant's Back, Calif.....	—	—	19	.77	—	—	—	—	19	6.6
Loveland Pass, Colo.....	13	.77	19	.88	—	—	5	8.0	14	8.9
Niwot Ridge, Colo.....	15	.78	—	—	—	—	13	5.2	—	—
Medicine Bow Mts., Wyo....	6	.69	20	.81	5	.80	2	8.5	20	5.7
Beartooth Mts., Wyo.....	24	.75	—	—	9	.86	13	2.0	—	—
Logan Pass, Mont.....	—	—	20	.89	9	.84	—	—	13	5.0
Highwood Pass, Alta.....	24	.70	10	.81	8	.71	15	2.5	4	3.8
Angel Glacier, Alta.....	—	—	—	—	9	.62	—	—	—	—
Summit Lake, B. C.....	25	.57	—	—	—	—	12	2.5	—	—
Donjek Mts., Yukon.....	9	.67	19	.57	9	.63	11	1.7	6	2.5
Eagle Summit, Alaska.....	29	.59	20	.53	9	.69	31	2.5	7	3.5
Pitmegea River, Alaska.....	14	.64	20	.52	—	—	19	3.0	—	—
Sagavanirktok River, Alaska..	12	.58	19	.60	9	.66	21	1.2	10	2.6
Pt. Barrow, Alaska.....	27	.46	—	—	9	.63	19	1.1	2	1.5
Thule, Greenland.....	—	—	—	—	5	.64	—	—	—	—

Location	FIELD Number of plants with stamen number of:			CHAMBERS Number of plants with stamen number of:			FIELD Number of plants with without rhizomes:		CHAMBERS Number of plants with without rhizomes:		
	2	variable	6	2	variable	6					
Elephant's Back, Calif.....	—	—	—	0	3	16	—	—	0	19	
Loveland Pass, Colo.....	12	1	0	14	0	0	0	7	0	20	
Niwot Ridge, Colo.....	10	1	2	—	—	—	0	8	—	—	
Medicine Bow Mts., Wyo....	0	0	3	2	0	18	0	5	0	20	
Beartooth Mts., Wyo.....	1	6	0	—	—	—	0	20	—	—	
Logan Pass, Mont.....	—	—	—	0	1	13	—	—	0	20	
Highwood Pass, Alta.....	0	0	14	0	0	4	2?	4	0	10	
Angel Glacier, Alta.....	—	—	—	—	—	—	—	—	—	—	
Summit Lake, B. C.....	0	0	6	—	—	—	1?	1	—	—	
Donjek Mts., Yukon.....	0	0	1	0	0	6	9	2	1	9	
Eagle Summit, Alaska.....	0	0	23	0	0	7	7	4	6	4	
Pitmegea River, Alaska.....	0	0	12	—	—	—	18	0	2	8	
Sagavanirktok River, Alaska..	0	0	16	0	0	11	17	1	7	3	
Pt. Barrow, Alaska.....	0	0	17	0	0	2	14	0	4	0	
Thule, Greenland.....	—	—	—	—	—	—	—	—	—	—	

thinly vegetated. Unstable fine-grained substrates such as eroding silt bluffs and solifluction lobes assume importance as *Oxyria* sites in Alaska and the Yukon. Vegetational cover in such sites is relatively high. *Oxyria* is not found in such habitats in the southern part of its range.

In general, the vegetational coverage of *Oxyria* microsites increases from south to north. The typical *Oxyria* habitat in the central Rocky Mountains or Sierra Nevada is a barren rocky talus, cliff, or bouldery morainal material. These "rock piles" have very little vegetation other than scattered *Oxyria* plants. For this reason, no quantitative vegetational sampling of *Oxyria* habitats was done south of Highwood Pass. The associates of *Oxyria* vary throughout its range in North America. At lower latitudes, southern alpine endemics are of importance. Toward the north, circumpolar species increase in frequency.

Trisetum spicatum, an arctic-alpine species of wide distribution, is often associated with *Oxyria* in both southern and northern habitats.

ANALYSIS OF MORPHOLOGICAL VARIABILITY BETWEEN POPULATIONS

The mass field collections¹ and the plants grown from seed in the greenhouse and in the growth chambers were analyzed to determine whether or not any patterns of morphological variability were associated with the geographic locations of the various populations. The following characteristics were measured: (1) maximum leaf width and length (top of petiole to apex of blade) of the largest leaf of a specimen; (2) number of primary branches of the largest inflorescence; (3) stamen number; (4) presence or

¹ All herbarium material, including mass collections, is deposited in the Duke University Herbarium.

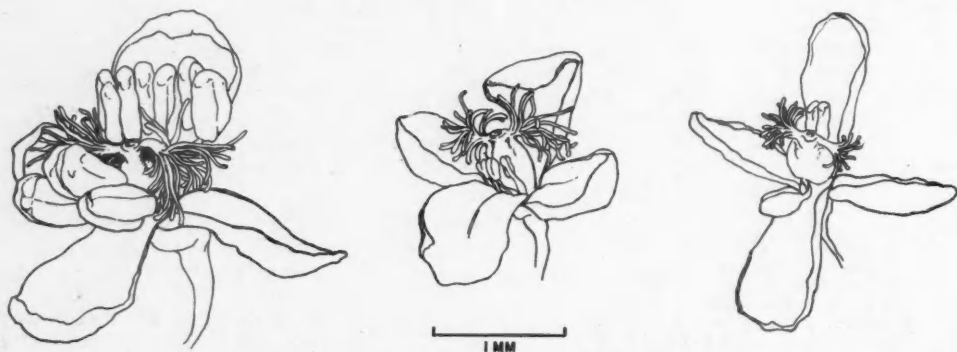


FIG. 3. *Oxyria* flower types. Flower on left has normal stamen development and is from a Sagavanirktok River, Alaska, plant. Center flower with aborted stamens is from a Logan Pass, Montana, plant. Two-stamen flower on right is from a Medicine Bow Mts., Wyoming, plant.

absence of rhizomes (Table 3). Also noted, was the number of flowers with stamens completely aborted in an inflorescence.

The average ratios of leaf length to leaf width appear to indicate the existence of two population groups: a northern one, made up of all the populations from Thule, Greenland, to Angel Glacier, Alberta, and a southern one, from Highwood Pass, Alberta, southward. Although the absolute magnitudes of the ratios are slightly altered by environmental conditions, the two groups are apparent under all treatments.

The average inflorescence branch number decreases from south to north. Plants of the far southern alpine populations are strikingly more branched than the northern forms, again suggesting two population groups rather than a cline.

Among *Oxyria* plants, certain individuals have unusual flowers which have only two stamens instead of the normal six. The inflorescences of these plants can be distinguished by their gross appearance. Other plants have inflorescences which have flowers with variable stamen numbers up to the full complement of six. Also, there are inflorescences containing from a few to all of the flowers with stamens completely aborted. The abortion of stamens does not appear to be directly related to the character of variable stamen number since the total complement of six undeveloped stamens can always be distinguished in such flowers. The principal flower types are illustrated in Figure 3.

Table 3, shows that the two-stamen character is limited to the far southern populations. The presence of two-stamen or variable-stamen forms also appears to separate the populations into southern and northern groups. In this instance, the separation occurs between Logan Pass, Montana, and Highwood Pass, Alberta.

Presence of rhizomes is another distinctive character of certain populations, which is not always easily noticed in the field, but is readily apparent in

cultivated *Oxyria* plants. Some populations have plants which produce rhizomes, while other populations lack this character entirely. In Table 3, it may be seen that at the extremes of the range investigated, rhizomes are either completely present or completely absent. The presence of rhizomes is frequent in plants of the northern populations, while plants of the south lack rhizomes. The relatively low percentages of rhizomatous forms in some northern populations grown in the environmental chambers may be a function of their lack of age when scored for this character. Young cultivated plants, when excavated,

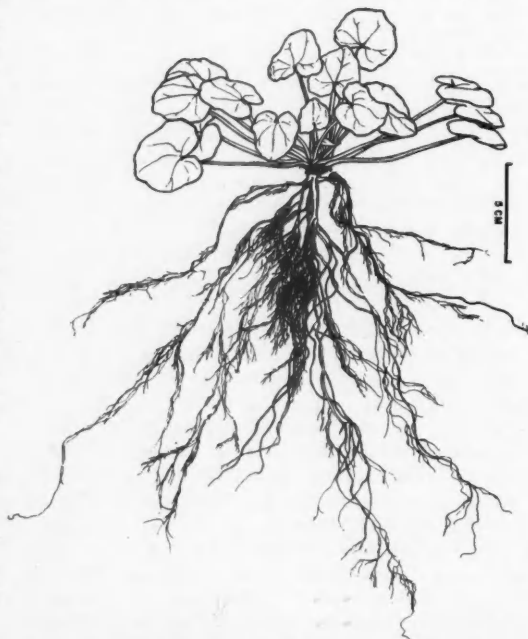


FIG. 4. Non-rhizomatous *Oxyria* plant grown from seed in the greenhouse. Seed collected from Beartooth Mts., Wyoming.

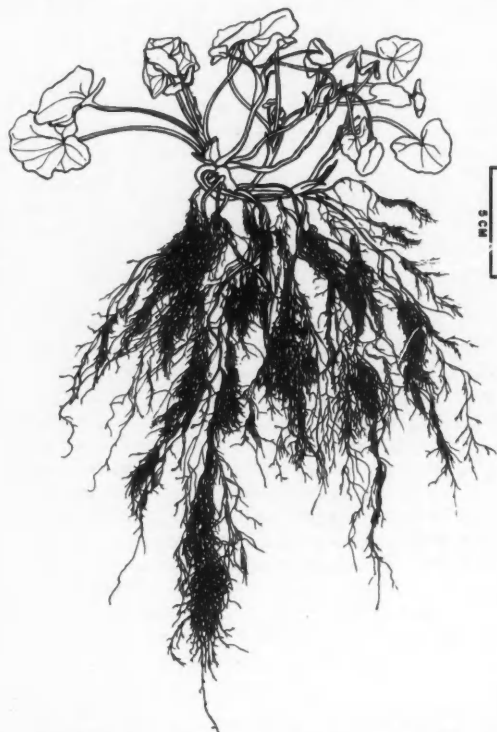


FIG. 5. Rhizomatous *Oxyria* plant grown from seed in the greenhouse. Seed collected from Sagavanirktok River, Alaska.

were often found to have rhizomes which were not yet apparent above the ground surface.

Figure 4 shows a pot-grown greenhouse-cultivated *Oxyria* from the Beartooth Mts., Wyoming, population. This nonrhizomatous form may be compared with a plant from the Sagavanirktok River, Alaska, population grown under the same conditions which is illustrated in Figure 5. The rhizomes originate at the base of the stem.

CHROMOSOME NUMBER

Published chromosome counts to date indicate that *Oxyria digyna* has $2n$ equaling 14 throughout its range. In Europe, counts have been made on material from Norway (Knaben 1950), France and Switzerland (Larsen 1954), as well as from the Kola Peninsula (Böcher & Larsen 1950). Counts have also been made on plants from Spitzbergen (Flovik 1940) and Iceland (Löve & Löve 1956). In North America, $2n$ equaling 14 has been found in Greenland and Canadian plants by Böcher & Larsen (1950). Other Greenland counts have been made by Holmen (1952) and Jørgensen, Sørensen & Westergaard (1958).

In the present work, flower buds were taken from plants grown under greenhouse and chamber condi-

tions and meiotic figures counted on the following populations: Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. This provides further evidence that *Oxyria* probably has the same chromosome number throughout its total range.

GERMINATION

A series of experiments was done to determine if there were any differences in the characteristics of seed germination among the various populations of *Oxyria*. All germination studies were made in duplicate on moist filter paper in petri dishes. Seeds were exposed to light during the course of all experiments unless otherwise noted. Results are expressed as the averages of the duplicate tests. Since no differences were found in the percentage of germination between achenes when either contained in, or removed from, the fruit, the single-seeded fruit was used as the test unit.

AFTER-RIPENING

To find out if *Oxyria* seed has an after-ripening requirement, fresh fruits were collected from inflorescences in several populations of cultivated plants and immediately placed in petri dishes, watered, and kept at 20°C . Additional seeds of some of the populations were stratified on moist filter paper for one week at 3°C before being placed at the 20°C temperature.

There was rather high viability (40 to 80%) in most of the populations even though the seeds were not allowed to dry and after-ripen. Although the seeds of these same populations when dried and stored in a freezer at -10°C for periods up to 2 yrs have slightly higher germination percentages than the fresh seed, there does not seem to be any appreciable after-ripening requirement. Cold-stratification of the freshly harvested seed results in only slightly higher germination percentages.

LIGHT AND DARK EFFECTS

To determine if *Oxyria* seeds have a light requirement for germination, replicate sets of field-collected seeds were placed in each of the following conditions: light at 20°C and dark at 20°C . The average percentage germination after 8 days is given in Table 4.

TABLE 4. Percentage germination in light and dark

Population	Light	Dark
Elephant's Back.....	82.5	2.5
Medicine Bow Mts.....	35.0	2.5
Beartooth Mts.....	52.5	15.0
Logan Pass.....	92.5	50.0
Highwood Pass.....	80.0	50.0
Donjek Mts.....	85.0	35.0
Eagle Summit.....	70.0	25.0
Pitmegea River.....	100.0	72.5
Sagavanirktok River.....	90.0	32.5
Pt. Barrow.....	67.5	35.0
Thule, Greenland.....	37.5	30.0

In all instances, there was higher percentage germination in the light than in the dark. The percentage increase of light germination over dark was variable for the different populations with little apparent pattern. However, the divergence between light and dark percentages was greatest for the far southern alpine populations.

EFFECT OF CONSTANT TEMPERATURE ON GERMINATION

Equal numbers of field-collected seeds of representative populations were placed in a graded series of constant temperatures, 3° C, 10° C, 15° C, 20° C, 25° C, and 30° C. After a two week period, no germination had occurred at 3° C and these seeds were moved to 20° C. The average relative germination (where the highest number germinating for a given population at any treatment equals 100%) at 14 days is given for all temperatures and populations in Table 5. Also shown is the germination of the 3° stratified seeds after one week at 20° C as a percentage of the maximum unstratified germination.

TABLE 5. Percentage germination of maximum at graded temperatures

Population	3°C	10°C	15°C	20°C	25°C	30°C	20°C stratified
Elephant's Back.....	0.0	17.1	80.0	100.0	62.9	28.6	94.3
Medicine Bow Mts.....	0.0	45.5	72.7	100.0	45.5	36.4	154.5
Beartooth Mts.....	0.0	3.8	53.8	100.0	46.2	19.2	103.8
Logan Pass.....	0.0	32.4	100.0	97.3	67.6	48.6	102.8
Highwood Pass.....	0.0	62.1	69.0	100.0	93.1	72.4	69.0
Donjek Mts.....	0.0	34.5	89.7	100.0	72.5	65.5	113.8
Eagle Summit.....	0.0	28.0	76.0	100.0	72.0	64.0	132.0
Pitmegea River.....	0.0	29.4	100.0	100.0	67.6	55.9	117.6
Sagavanirktok River.....	0.0	11.1	74.1	100.0	77.8	55.6	129.6
Pt. Barrow.....	0.0	7.7	80.8	100.0	73.1	50.0	107.7
Thule, Greenland.....	0.0	7.7	69.2	100.0	46.2	53.8	76.9

Several generalizations may be made from this table. In all but the Logan Pass population, the maximum germination occurs at 20° C. Germination is less at 10° C than at 30° C in all but the Medicine Bow Mts. population. Lastly, in most populations, the germination of stratified seeds was higher than the maximum germination percentage of unstratified seeds after 2 weeks at 20° C.

EFFECT OF ALTERNATING TEMPERATURES ON GERMINATION

A more natural situation was provided for germination by placing equal numbers of seeds of two alpine populations and two arctic populations in the alpine and in the arctic growth chambers where they were subject to the influence of alternating temperatures. The average percentage germination at 3 weeks for these populations in the 2 chambers is shown in Table 6. In all instances, germination was lower in the arctic chamber than in the alpine. However, it may be significant that the germination of the arctic populations was less reduced than those of alpine populations in the arctic chamber, with its colder day and night temperatures.

TABLE 6. Percentage germination in "arctic" and "alpine" diurnal temperature cycles

Population	"Arctic"	"Alpine"	Arctic as percent of alpine
Elephant's Back.....	12.5	42.5	31.0
Logan Pass.....	32.5	87.5	37.2
Pitmegea River.....	65.0	80.0	81.4
Sagavanirktok River....	40.0	70.0	57.0

GROWTH AND DEVELOPMENT

EFFECT OF CONTROLLED ENVIRONMENTS ON GROWTH

Laboratory measurements of rates of petiole elongation, leaf expansion, and leaf production were made on 5 Oxyria populations: Loveland Pass, Highwood Pass, Donjek Mts., Eagle Summit, and Pitmegea River. These rates were measured on 10 individuals of each population in each of the two growth chambers, arctic and alpine. All of the plants were grown from seed and were 2 months old at the time of first measurement. The initial and final measurements for a 10-week period are given in Table 7.

TABLE 7. Growth measurements of Oxyria plants under controlled regimes*

Population and regime	MEAN PETIOLE LENGTH		MEAN LEAF WIDTH		MEAN LEAF NUMBER	
	Initial	Final	Initial	Final	Initial	Final
Loveland Pass						
Alpine chamber.....	1.7	9.9	0.9	4.0	4.2	27.1
Arctic chamber.....	1.6	7.2***	1.0	3.5	4.0	23.2
Highwood Pass						
Alpine chamber.....	1.6	5.2	1.0	2.9	6.0	45.8
Arctic chamber.....	1.8	7.2	1.1	3.0	6.6	45.9
Donjek Mts.						
Alpine chamber.....	1.9	3.7	1.3	2.2	4.8	17.0
Arctic chamber.....	1.8	7.2***	1.2	3.3***	4.7	27.1**
Eagle Summit						
Alpine chamber.....	1.6	3.0	1.1	2.0	4.5	12.9
Arctic chamber.....	1.4	5.3***	1.0	2.4	4.5	13.6
Pitmegea River						
Alpine chamber.....	1.7	2.3	1.0	1.5	3.8	11.4
Arctic chamber.....	1.9	4.8***	1.0	2.0***	4.9	14.6

* All measurements in centimeters.

** Significant difference between means (5% level).

*** Highly significant difference between means (1% level).

The average initial petiole length in all populations was essentially the same. The final petiole length on plants in the alpine chamber decreased progressively from the southern to the northern populations. On the other hand, the terminal measurements on populations in the arctic chamber fell into two groups. Plants from the 3 southernmost populations had identical averages, 7.2 cm, while the 2 northernmost populations averaged 5.3 and 4.8 cm. The Loveland Pass population, of far southern alpine origin, was the only one to have longer petioles in the alpine chamber than in the arctic; this difference was significant at the 1% level.

Initial measurements on leaf width were similar for all of the populations, although Eagle Summit plants had slightly wider leaves. The final measurements on leaf width showed the same trends as those shown by petiole length. In the alpine chamber, the widths decreased from south to north. In the arctic chamber, there were two groups: the 3 southernmost populations had average measurements in the 3 cm region, whereas the 2 northern populations had averages in the 2 cm region. Again, Loveland Pass was the only population with larger measurements in the alpine chamber.

Later, evidence will be presented which indicates that the comparison of the populations in the alpine chamber is actually an expression of a clinal growth response to photoperiod. On the other hand, in the arctic chamber where all of the populations had an ample photoperiod for growth and flowering, the differences between populations are an expression of genetically based morphological differences.

A comparison between treatments of the averages of leaf width and petiole length shows that, in the southernmost alpine population, the maximum development in these characters was in the alpine chamber. For the other populations, the opposite was true, with greater development in the arctic chamber. The Loveland Pass population was the only one in this experiment which came from an environment with a maximum photoperiod of less than 15 hrs, the photoperiod regime of the alpine growth chamber. This may explain the growth trend reversal for this population in comparison with the others.

The data on leaf number are similar in all respects to those of leaf expansion and petiole elongation with one major exception. The Highwood Pass population had a very high number of leaves in both treatments, almost twice that of any other population in either treatment. This acclinal variant somewhat obscures, but does not negate, the trends already discussed.

In Figure 6, representatives of the populations are arranged with the southernmost on the left extending latitudinally to the northernmost on the right. These plants had all been in the arctic or alpine chambers for three months at the time of the photographs, not long enough for most populations to flower. The clinal growth rate from south to north is well-illustrated.

EFFECT OF CONTROLLED ENVIRONMENTS ON PHENOLOGICAL DEVELOPMENT

A second group of populations was grown in the controlled chambers and the plants were scored at weekly intervals for phenological development.

In this group of populations were Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. Ten members of each population were placed in each of the arctic, alpine, and constant growth chambers. These chambers had the following temperature and light regimes: alpine chamber, 15-hr photoperiod, 12-hr day temperature of 65° F and a 12-hr 40° F night temperature; arctic chamber,

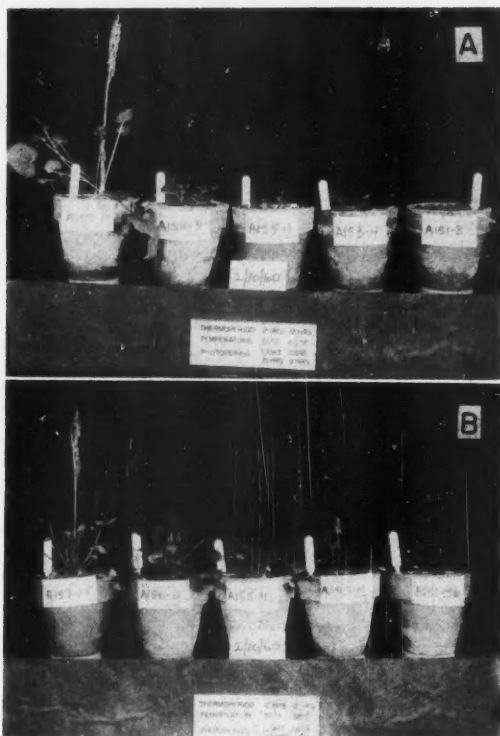


FIG. 6. Aspects of plants from a latitudinal collection of populations grown under uniform conditions. Origin from left to right: Loveland Pass, Highwood Pass, Donjek Mts., Eagle Summit, Pitmegea River. Photograph A is from the alpine chamber; photograph B from the arctic chamber. Plants had been under controlled conditions for only 3 months, not long enough for most populations to produce flowering plants.

24-hr photoperiod, 12-hr temperature period of 55° F and a 12-hr temperature of 35° F; constant temperature chamber, 12-hr photoperiod and a 24-hr thermoperiod of 50° F.

At the beginning of the experiment, all plants were 4 month old pre-floral seedlings. The first plants started coming into flower after being in the chamber for 2 months. In Table 8 are given the weekly flowering or fruiting percentages of each population in each of the 3 chambers.

Both the Elephant's Back and Medicine Bow Mts. populations occur in environments which have a maximum photoperiod of 15 hrs or less. Logan Pass has a natural maximum photoperiod of approximately 16 hrs, and Sagavanirktok River has over 2 months of continuous light in midsummer.

In the constant temperature growth chamber, while it was set on a 12-hr photo-period, no plants of any population flowered.

In the alpine chamber (both Elephant's Back and Medicine Bow Mts. populations quickly attained a 100% flowering condition. Most of the Logan Pass

TABLE 8. Percentages of plants in four populations flowering or fruiting at end of weekly intervals

Time in weeks	ELEPHANT'S BACK		MEDICINE BOW MTS.		
	Alpine	Arctic	Constant	Alpine	Arctic
1	0	0	0	0	0
2	0	0	0	10	0
3	30	10	0	30	0
4	60	20	0	30	30
5	80	60	0	30	30
6	90	60	0	80	70
7	90	80	0	80	80
8	100	80	0	80	100
9	100	80	0	90	100
10	100	80	0	90	100
11	100	80	0	100	100
12	100	100	0	100	100
13	100	100	0	100	100
14	100	100	0	100	100
15	100	100	0	100	100
16	100	100	0	100	100
17	100	100	0	100	100
18	100	100	0	100	100

Table 8 (continued)

Time in weeks	LOGAN PASS			SAGAVANIRKTOK RIVER		
	Constant	Alpine	Arctic	Constant	Alpine	Arctic
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0	0	0	0	0	20
4	0	0	10	0	0	30
5	0	10	10	0	0	40
6	0	10	30	0	0	70
7	0	20	60	0	0	80
8	0	20	90	0	0	100
9	0	20	90	0	0	100
10	0	20	90	0	0	100
11	0	30	90	0	0	100
12	0	30	90	0	0	100
13	0	40	90	0	0	100
14	0	50	90	0	0	100
15	0	50	100	0	0	100
16	0	50	100	0	0	100
17	0	50	100	0	0	100
18	0	50	100	0	0	100

plants were considerably retarded. Only 50% of the individuals had reached a flowering condition 4 months after the first plants of any populations had flowered. The Sagavanirktok River population failed to flower or fruit at all in the alpine chamber.

Thus, in the alpine chamber there appeared to be a latitudinal ecotypic response to a 15-hr photoperiod. Those populations which have a natural photoperiodic maximum of 15 hrs or less, produced flowers and fruits normally. The Logan Pass population, originating from an area which has a natural maximum photoperiod of 16 hrs, has some members which do flower and others which do not flower and fruit normally at the 15-hr photoperiod. Finally, the Sagavanirktok River population, whose natural environment has a maximum photoperiod considerably in

excess of 15-hrs, completely fails to flower or fruit under so short a photoperiod.

In the arctic chamber, which had a continuous



FIG. 7. Plants from Elephant's Back, California, population grown under controlled alpine (A) and arctic conditions (B).

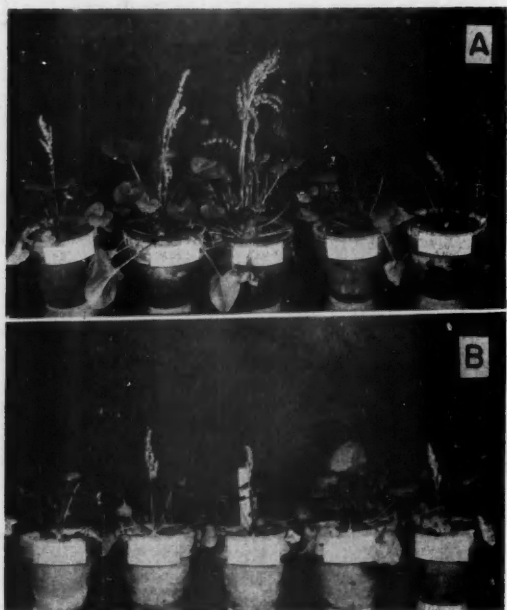


FIG. 8. Plants from the Medicine Bow Mts., Wyoming, population grown under controlled alpine (A) and arctic conditions (B).

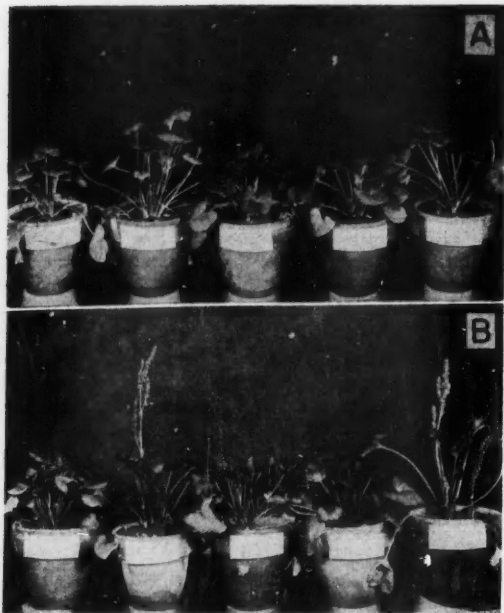


FIG. 9. Plants from the Logan Pass, Montana, population grown under controlled alpine (A) and arctic conditions (B).

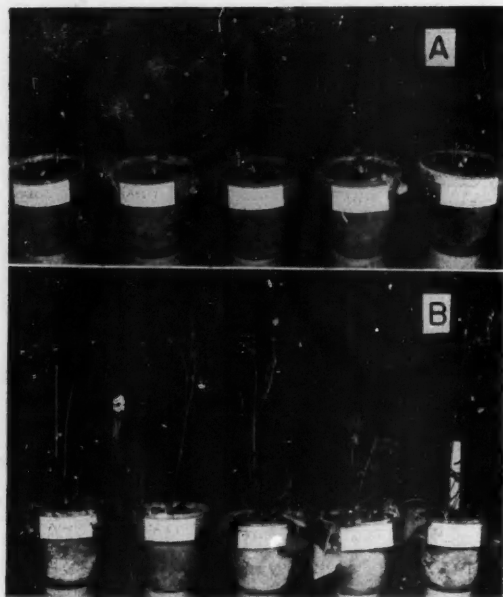


FIG. 10. Plants from the Sagavanirktok River, Alaska, population grown under controlled alpine (A) and arctic conditions (B).

photoperiod, all populations came into flower relatively quickly.

The general aspect of the plants grown during this experiment in the arctic and alpine chambers is shown

in Figures 7, 8, 9, and 10. These photographs were all taken on the same day, immediately prior to the first date of inflorescence harvest.

Although there is evidence that temperature may limit photoperiodic induction in some plants (Thomas 1956), there was probably no significant difference in such induction between *Oxyria* plants in the arctic and alpine growth chambers due to temperature alone. There was only a 5° F difference in the minimum daily temperatures of the two chambers and 10° in the maximum. There is no way of evaluating the temperature effect on photoinduction from the present data. However, the fact that flowering in most populations did *not* occur in the higher mean temperature (52.5° F) of the alpine chamber but did occur in the lower mean temperature (45° F) of the arctic chamber, does appear to indicate that low temperature was not limiting.

At the conclusion of the first experiment, the photoperiod of the constant growth chamber was shifted from 12 to 17 hrs, but the temperature was maintained at 50° r'. While the plants were on the 12-hr photoperiod, they all formed perennating buds at the soil surface but maintained functional leaves; in effect, they rosetted. Near the conclusion of the 12-hr photoperiod experiment, the temperature of the constant chamber accidentally dropped to 15° F for a 12-hr period. This low temperature damaged the functional leaves but not the perennating buds. When this chamber was switched to a 17-hr photoperiod, the plants very rapidly broke bud dormancy and became vegetative. In 3 weeks time, the first plants had come into flower.

The populations represented in the constant chamber included the Medicine Bow Mts., Logan Pass, Eagle Summit, and Sagavanirktok River. Thus, the group differed from the one present in the arctic and alpine chambers by lacking Elephant's Back and having the additional Eagle Summit population. The flowering percentages of each population during the 17-hr photoperiod experiment in the constant chamber are given in Table 9. Only the 2 southern populations displayed flowering activity. The 17-hr photoperiod of the constant growth chamber was nearest to the natural 16-hr photoperiod of the Logan Pass

TABLE 9. Percentage of plants in flower at weekly intervals in the constant chamber under 17 hour photoperiod

Time in weeks	Medicine Bow Mts.	Logan Pass	Eagle Summit	Sagavanirktok River
1	0	0	0	0
2	0	20	0	0
3	0	60	0	0
4	0	80	0	0
5	0	80	0	0
6	0	80	0	0
7	20	100	0	0
8	60	100	0	0

population. The fact that this population flowered first in this chamber indicates how closely adjusted these populations are to the natural summer day-length at their respective latitudes. The Medicine Bow Mts. population, with a natural maximum photoperiod of 15-hrs, although flowering, was significantly delayed in comparison to the Logan Pass plants.

INFLORESCENCE PRODUCTION

The total inflorescence production of the populations in the first group was tabulated for a 5-month period (Table 10). The data are expressed as the average number of inflorescences harvested per plant during the total time period and do not represent the number present on a plant at any given time. The production was tabulated only for plants in the arctic chamber where all populations had an ample photoperiod for flowering. The 5-month period commenced with the time of appearance of the first inflorescence in the whole group of populations.

TABLE 10. Inflorescence production of selected populations in the arctic chamber over a five-month period

Population	Average number of inflorescences produced per plant
Elephant's Back.....	24.9
Medicine Bow Mts.....	21.2
Logan Pass.....	10.3
Sagavanirktok River.....	7.7

There is a distinct decrease in inflorescence production from southern to northern populations. This trend in inflorescence production would be considerably magnified if the data were converted to relative seed production. This is because of the south to north decrease in inflorescence branching which was discussed earlier in the analysis of morphological variability.

In the field, there appears to be a decrease in the importance of seed production in the north. At the far northern end of its range, in Peary Land, Greenland, *Oxyria* was not observed to set fruit (Holmen, 1957). The trend of increased rhizome production in the north has already been shown and likely compensates to some extent for reduced seed production.

It should be pointed out that the 5-month span of observation would constitute at least two growing seasons in the field. Thus, the production during such a prolonged growing period is not an index to actual field production, but shows at least a probable genetic difference between populations.

The fact that plants were kept in a continuously flowering condition for periods of up to a year in the growth chamber indicates that there is no inherent seasonal periodicity in the reproductive process.

DORMANCY

Under a 12-hr photoperiod, in the growth chambers, perennating buds were formed. Functional

leaves, however, were retained until the advent of subfreezing temperatures.

A similar situation prevailed in greenhouse-grown plants. In the fall, *Oxyria* plants produced perennating buds and maintained this condition throughout the winter in spite of warm greenhouse temperatures. Several or no functional leaves were retained on these plants. *Oxyria* could be brought out of this dormant state by extending the photoperiod to 24 hrs without altering the temperature regime. During the winter, in the greenhouse, the temperature never fell below 38° F. However, plants kept outside under a 24-hr photoperiod and subjected to night temperatures as low as 24° F did not break dormancy until warmer temperatures prevailed.

A short photoperiod, then, will induce perennating bud formation even under the influence of relatively high temperatures. Long photoperiods will bring the plants out of this dormant state unless they are subjected to unfavorably low temperatures.

PHOTOSYNTHESIS AND RESPIRATION

FIELD RATES

The rate of apparent photosynthesis of intact *Oxyria* plants was measured twice in the field. Both test periods were made at mid-day during July, 1958, in the Medicine Bow Mts. at an elevation of 10,800 ft.

There was a rather wide fluctuation in the photosynthetic rate and also in temperature and solar radiation which were measured simultaneously. Such variation is rather typical for such regions where variable afternoon cloudiness during the summer is a regular occurrence. The maximum observed photosynthetic and respiration values for both test periods are given in Table 11, expressed on fresh weight, square decimeter, and milligram of total chlorophyll bases.

TABLE 11. Maximum observed field rates of photosynthesis and respiration

	Per gm fw/hr	Per dm ² /hr*	Per mg chlorophyll/hr	Chamber temperature (°C)	Light (f. c.)
Photosynthesis					
July 9.....	3.65	5.79	9.73	31	8,700
July 22.....	3.74	7.39	7.52	25	9,000
Respiration					
July 9.....	0.85	1.35	2.27	21	0
July 22.....	0.18	0.35	0.35	14	0

* Leaf areas throughout this study were calculated as the sum of both upper and lower surfaces.

To find out if it was possible to distinguish roughly between light and temperature effects on photosynthetic rate, all of the 5-minute interval rates from both the July 9 and July 22 test periods were pooled and plotted against the chamber temperature and are presented in Figure 11. With the exception of several apparently aberrant values, a rough temperature-

dependent photosynthetic curve is formed. The aberrant values all represent photosynthetic rates occurring at light intensities of 1,800 fc or less, and may, therefore, represent light-dependent values, at least for the temperature range examined. Since 2,000 fc values fall into the temperature-dependent curve, photosynthetic light saturation in the field apparently occurs at approximately 1,900 to 2,000 fc.

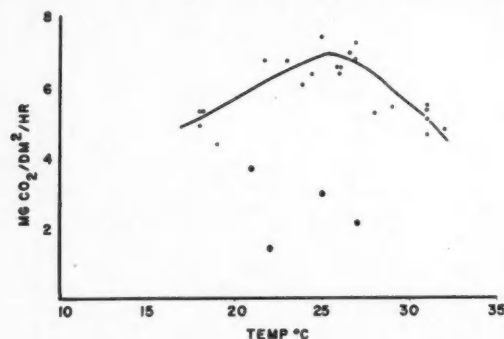


FIG. 11. Relationship between field photosynthetic rate and chamber temperature. Open circles are photosynthetic values occurring at 1,800 fc or less.

Wager (1941) reports a maximum observed photosynthetic rate for this species in East Greenland as 9.0 mg/dm² (leaf surface)/hr which is a little above the 7.4 mg/dm²/hr peak observed in the Medicine Bow Mts. The estimated average light saturation value from Wager's light curves is approximately 1,800 fc, which is comparable to the estimated value from the Medicine Bow Mts. Wager also gives respiration values for *Oxyria* on a gram fresh weight basis for 0° C, 10° C, and 20° C, which are respectively 0.10, 0.31, and 0.52 mg/gfw. The two respiration values given in Table 11 for the Medicine Bow Mts. fall above and below the expected magnitude by interpolation into Wager's curve.

FIELD CHLOROPHYLL MEASUREMENTS

The averaged chlorophyll values on a fresh weight and a leaf area basis are given in Table 12 for populations from the Medicine Bow Mts., Wyoming, and Eagle Summit, Alaska. The Medicine Bow values represent an average of 5 determinations. There were only 2 determinations from Eagle Summit, since some samples were lost in transit. From these limited data, it appears that plants from the low elevation, more northerly, Eagle Summit population have a higher total chlorophyll content on both a fresh weight and leaf area basis than plants from the high elevation populations of the Medicine Bow Mts. far to the south.

LABORATORY RATES

A primary objective in the laboratory gas exchange measurements was to determine if differences in photosynthesis and respiration rate potentials exist among

TABLE 12. Chlorophyll contents of field-collected leaves

	Medicine Bow Mts.	Eagle Summit
mg. C/gm. f.w.....	.387	.636
mg. C/dm ²674	.867

Oxyria populations. A secondary concern was the evaluation of the effects of the controlled alpine and arctic environments on these particular processes.

All photosynthetic values presented here are of apparent or net photosynthesis which is equal to gross photosynthesis minus the "light" respiration value.

Two types of compensation points are considered. One, the light compensation point, is that light value, at a given temperature, where the net photosynthetic rate is equal to zero, i.e., the gas exchange is balanced. The other, the temperature compensation point, is used here in the sense of Transeau, Sampson & Tiffany (1940), as that temperature, at a given light intensity, where the apparent photosynthesis rate intersects or equals the dark respiration rate. Actually, on any given temperature-dependent photosynthetic curve, there would be two such compensation points, the upper and the lower. No lower temperature compensation points were determined in this study. The upper temperature compensation point, as used here, is not actually a true compensation point since the gas exchange is not balanced in the photosynthetic organ; gross photosynthesis is progressing at twice the respiration rate. The upper temperature at which gross photosynthesis and respiration are equal (the true temperature compensation point) would presumably be near the lethal temperature limit for the plant and would be difficult to determine.

EFFECT OF CONTROLLED ENVIRONMENTS ON PHOTOSYNTHESIS AND RESPIRATION

A series of determinations of photosynthesis at 20° C and dark respiration at 15° C were made on even-aged plants from both the alpine and arctic growth chambers representing four populations: Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River. All the plants in this series from the arctic chamber had flowered, as had those from the alpine chamber with the exception of the Alaskan population, which was held in a non-flowering condition by the 15-hr photoperiod.

The 20° C determinations are expressed on a leaf area basis and are presented in Figure 12 as averages of three or four determinations, each from a different plant. In all instances, the photosynthetic rate of plants in the arctic treatment was less than that of similar plants in the alpine treatment. This difference is, in all probability, a response to the high leaf carbohydrate status of the plants grown in the arctic chamber.

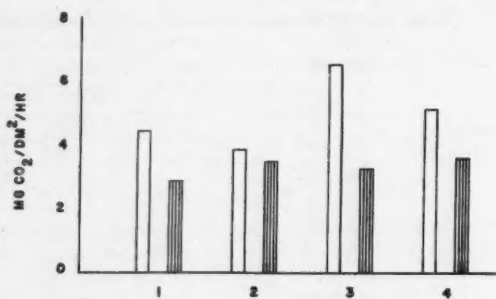


FIG. 12. Average laboratory-determined photosynthetic rates at 20°C on a leaf area basis. Unshaded bars for plants grown in the alpine chamber; shaded bars, plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Sagavanirktok River, Alaska.

The average photosynthetic rates at 20°C of plants from all populations in the arctic chamber were surprisingly constant, varying between approximately 3 to 3.5 mg CO₂/dm²/hr. There was, however, considerable variation in the values from the plants in the alpine chamber. Although these plants were even-aged, they were not equally developed since the Logan Pass plants were considerably retarded in flowering and those from Sagavanirktok River were not fruiting at all because of the relatively short photoperiod. It may be that the difference observed in the average photosynthetic rates of plants from the alpine chamber were responses to their unequal developmental stage which in turn was an ecotypic response to short (15 hrs) photoperiod.

These same results, when expressed on a milligram of chlorophyll basis, show a striking reduction in the average Assimilation Number (photosynthetic rate on a unit chlorophyll basis) of the Sagavanirktok River population, irrespective of treatment, as illus-

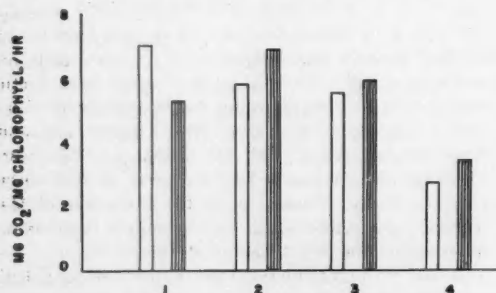


FIG. 13. Average laboratory-determined photosynthetic rates at 20°C on a chlorophyll basis. Unshaded bars refer to average population rates of plants grown in the alpine chamber. Shaded bars refer to average rates of plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Sagavanirktok River, Alaska.

trated in Figure 13. This will be discussed at greater length when the results of the leaf chlorophyll contents of the various populations are presented.

The determinations of the dark respiration rates at 15°C represent averages of 5 replications on each population from each treatment, and also include an additional Alaskan Population, Eagle Summit. The results are shown in Figure 14, where the averages are expressed on a mg CO₂/gfw/hr basis.

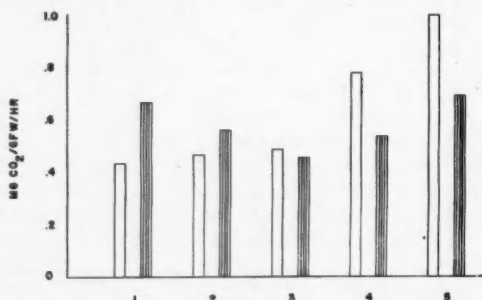


FIG. 14. Average laboratory-determined respiration rates at 15°C on a fresh weight basis. Unshaded bars refer to average population rates of plants grown in the alpine chamber. Shaded bars refer to average rates of plants grown in the arctic chamber. Numbers refer to the following populations: 1. Elephant's Back, California, 2. Medicine Bow Mts., Wyoming, 3. Logan Pass, Montana, 4. Eagle Summit, Alaska, 5. Sagavanirktok River, Alaska.

The results of the respiration measurements are somewhat difficult to interpret. Alpine chamber plants from the two Alaskan populations showed markedly higher respiration rates than southern plants from the same chamber. In the alpine chamber, respiration rate increased latitudinally from southern plants to northern plants. The real difficulty lies in explaining the effect of either treatment in respect to the other. The results may be viewed, perhaps, as a respirational imbalance produced by environmental displacement. The 3 southern alpine populations had a slightly increased respiration rate when grown in the arctic chamber. The two northern or Alaskan populations had an increased respiration rate when grown in the alpine chamber. Apparently, the greater the geographical displacement, the greater the imbalance. A complicating factor may have been the differential development of the plants, since the two northern populations in the alpine chamber remained in a vegetative condition.

EFFECT OF CONTROLLED ENVIRONMENT ON CHLOROPHYLL CONTENT

After being used in the gas exchange determinations, the leaves of plants from the arctic and alpine chambers were analyzed for total chlorophyll. The averaged values in milligrams of chlorophyll are given both on a per gram fresh weight and a leaf area basis in Table 13. The trend among popula-

TABLE 13. Leaf chlorophyll content of *Oxyria* plants grown under controlled conditions

Population	ARCTIC CHAMBER		ALPINE CHAMBER	
	mg/gm	mg/dm ²	mg/gm	mg/dm ²
Elephant's Back.....	.32	.50	.33	.62
Loveland Pass.....	.30	.67	—	—
Medicine Bow Mts.....	.32	.53	.45	.65
Logan Pass.....	.30	.56	.64	1.10
Donjek Mts.....	.34	.74	—	—
Eagle Summit.....	—	—	1.38	1.90
Sagavanirktok River..	.52	.97	1.27	1.89
Pt. Barrow.....	.50	.85	—	—

tions appears comparable using either basic unit. The results, therefore, will be discussed in general terms.

In comparing chlorophyll contents under the two treatments, the difference between chambers was greater in the northern populations which had higher values in the alpine chamber. This effect is probably related to the non-flowering condition of the arctic populations in the alpine chamber. Among the populations that flowered in both chambers, there was little difference in chlorophyll content.

A comparison among populations within either chamber showed higher average chlorophyll content in the northern plants. In spite of the higher concentration of chlorophyll in the northern populations, there was little difference in the photosynthetic rate at 20° C on a leaf area basis. This results in an apparent decrease in assimilation number, or decrease in photosynthetic efficiency per unit of chlorophyll, in these populations.

COMPARISON OF FIELD AND LABORATORY RESULTS

Extrapolation of laboratory results to field situations should be made with great care. A minimum requirement for such extrapolation should be an analysis of the relative effect of the laboratory environment on the basic physiological responses of the organism as compared to the effect of the natural environment. An attempt has been made to assemble data of this sort in the present study.

PHOTOSYNTHESIS AND RESPIRATION

Table 14 shows the maximum rates of photosynthesis and dark respiration observed in the field and in the laboratory for plants of the Medicine Bow Mts. population. The laboratory rates are from 20° C determinations, which approximates the temperature of the field determinations. The photosynthetic rates agree very closely on both a gram fresh weight and milligram of chlorophyll basis. The laboratory rate on the basis of a square decimeter of leaf area is less than that from the field. There is very close agreement between the respiration rates from the field and the laboratory.

Although caution must be exercised in the use of such single values by themselves, they do indicate that the laboratory photosynthesis and respiration

TABLE 14. Maximum observed rates of photosynthesis and respiration in field and laboratory in *Oxyria* plants from the Medicine Bow Mountains

	mg CO ₂ /gfw/hr	mg CO ₂ /dm ² /hr	mg CO ₂ /mg chlorophyll/hr
Photosynthesis			
Field.....	3.74	7.39	9.73
Laboratory.....	3.98	5.60	10.29
Respiration			
Field.....	0.83	1.13	—
Laboratory.....	0.85	1.35	—

rates of *Oxyria* plants grown in simulated environments are of the same order of magnitude as those of *Oxyria* plants in their native habitat.

Both Russell (1940b) and Warren Wilson (1959, 1960) have published net assimilation rates for *Oxyria* from Jan Mayen Island based on carbohydrate increase in detached leaves. Russell gives a figure of 0.30 g/dm²/wk. Warren Wilson using leaves from a single source reports 0.34 g/dm²/wk for leaves exposed on a windswept summit and 0.46 g/dm²/wk for those in a sheltered hollow. His other measurements, using *Oxyria* from various habitat types, range from 0.54 g/dm²/wk to 0.66 g/dm²/wk. Most measurements on Jan Mayen were made in late August on plants which probably were in fruiting or post-fruiting condition.

These Jan Mayen net assimilation results were compared with an approximated value calculated from photosynthesis and respiration rates of plants of the Eagle Summit and Sagavanirktok River populations grown in the arctic chamber. A photoperiod of 17.5 hrs was selected for the calculations. This photoperiod approximates that at latitude 71°N on the 21st of August. Average net photosynthesis at 10° C was used to approximate day-time gain. To calculate night time loss, 5° C dark respiration values were used. Warren Wilson (1960) reports mean maximum and mean minimum August temperatures from Jan Mayen as 8.8° C and 4.9° C, respectively. Warren Wilson (1957) also gives temperatures for a similar period in August for Resolute, Cornwallis Island, 4° in latitude north of Jan Mayen Island. Air temperatures 1 cm above the ground for a diurnal period at Resolute had an approximate maximum of 6° C and a minimum near 2° C. Bliss (1956) gives mean 4 a.m. air temperatures of 2° C for late August and noon values at 8° C for 5 cm above the ground in an arctic habitat (Umiat, Alaska) 3° in latitude south of Jan Mayen. If anything, then, the temperature values selected for calculation are a bit high. Seventy per cent was used as the conversion factor for converting CO₂ fixed to carbohydrate produced.

The net assimilation rate of our laboratory grown plants was calculated to be 0.53 g/dm²/wk. This is very close to the quoted field rates. Single-surface leaf area was used as the basis in this instance so as to conform with the techniques used on Jan Mayen.

Both Russell and Warren Wilson emphasize the approximate nature of their field-determined net

assimilation rates. Russell says that these values should be considered as a minimum of the actual potential. Yet, the agreement between the calculated and field rates is quite good.

CHLOROPHYLL CONTENT

The average field values for leaf chlorophyll in plants of the Medicine Bow Mts. population were 0.39 and 0.67 mg on a gram fresh weight and a square decimeter of leaf area basis, respectively. The average chlorophyll values from cultivated plants of this population from the alpine chamber were 0.45 and 0.65, respectively. The close agreement between the field and laboratory chlorophyll values is obvious.

The Eagle Summit chlorophyll contents from field-grown plants, 0.52 mg C/gfw and 0.97 mg C/dm², can be compared with the values of 0.67 and 0.87 from Sagavanirktok River plants grown in the arctic chamber. There are no available arctic chamber chlorophyll values for Eagle Summit. Again, the agreement is fairly close but not so close as in the Medicine Bow Mts. chlorophyll contents.

POPULATION DIFFERENCES IN PHOTOSYNTHESIS AND RESPIRATION RATES IN RESPONSE TO TEMPERATURE

A somewhat more detailed study of the apparent differences between the rates of photosynthesis and respiration of the populations was made by constructing temperature curves for these processes. To insure equally developed plants, even-aged fruiting specimens from the arctic chamber were utilized. Determinations were made at temperatures ranging from 0° C to over 40° C. Unfortunately, at the 2,100 fc light intensity utilized for these determinations, 10° C was the lowest temperature that could be maintained for photosynthetic measurements. This was due to the inadequacy of the chamber cooling system.

The general shapes of the photosynthesis-temperature curves were similar for the three southern alpine populations, with maximum rates occurring at the same temperatures. The photosynthesis curves for the two northern populations had peaks at lower temperatures than those of the alpine plants. The actual average photosynthesis rates of the different populations were somewhat variable at any given temperature. In order to present more representative average rates without affecting the characteristics of the curve, the results from the 3 southern alpine populations were pooled and those from the two Alaskan populations were also pooled. Determinations within 5° C intervals were considered as a class. The values derived, representing in some instances as many as 9 separate determinations, are presented in Figure 15.

A number of important differences are apparent in a comparison of the curves for the southern and northern populations. First, the photosynthetic peak in the northern populations is at a lower temperature, although the maximum photosynthetic rate is essentially the same in both groups. Second, the

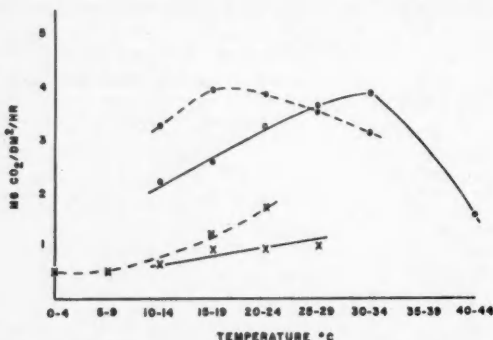


FIG. 15. Average photosynthetic and respiration rates of a southern alpine population group (Elephant's Back, Medicine Bow Mts., and Logan Pass), and of a northern population group (Eagle Summit and Sagavanirktok River), at different temperatures. Solid circles refer to average photosynthetic rates of the southern group; open circles, average photosynthetic rates of the northern group; circled X's, average respiration rates of the northern group; X's, average respiration rates of southern group.

respiration rate in the northern population is considerably higher, particularly at the higher temperatures.

The separated photosynthetic peaks and the different respiration rates result in a difference in the upper temperature compensation points. This may be seen by extrapolation of the curves. Actual determinations of the upper temperature compensation point yielded an average of 35° C (4 determinations) for the southern alpine group and 27° C for the northern populations (2 determinations). These actual determinations thus confirm that the compensation points are quite different.

To investigate further the apparent dissimilarity between northern and southern groups, two additional populations were tested. Temperature curves

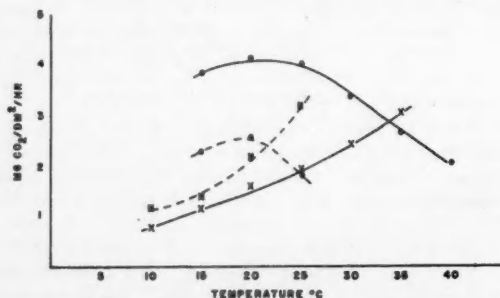


FIG. 16. Average photosynthetic and respiration rates of a southern alpine population, Loveland Pass, Colorado, and a northern population, Donjek Mts., Yukon Territory, at various temperatures. Average photosynthetic rates: solid circles, plants from the Donjek Mts.; open circles, plants from Loveland Pass. Average respiration rates: circled X's, plants from the Donjek Mts.; X's, plants from Loveland Pass.

were plotted from gas exchange measurements on even-aged pre-floral plants grown in the arctic chamber from Loveland Pass, Colorado, and the Donjek Mts., Yukon Territory. The average results of triplicate analyses for each series are given in Figure 16 on a $\text{mg CO}_2/\text{dm}^2/\text{hr}$ basis.

Although the plants were of the same age, they had exhibited a marked inequality in growth rate, which was probably a reflection of the differences of the photosynthetic rates. Aside from this, the essentials of the curves for the two population types are the same as presented earlier, that is, different temperatures for maximum photosynthetic rate, and a large difference in respiration rate. As a result, the upper temperature compensation points are decidedly different; the northern race reached compensation at about 22° and the southern race at 35° C.

POPULATION DIFFERENCES IN PHOTOSYNTHETIC RESPONSE TO LIGHT

Duplicate determinations of photosynthetic rate were made for an arctic and an alpine population at light intensities ranging from 55 to 5,200 fc. The determinations were made at 20° C on plants from Loveland Pass and the Donjek Mts. The resultant photosynthesis-light curves are presented in Figure 17.

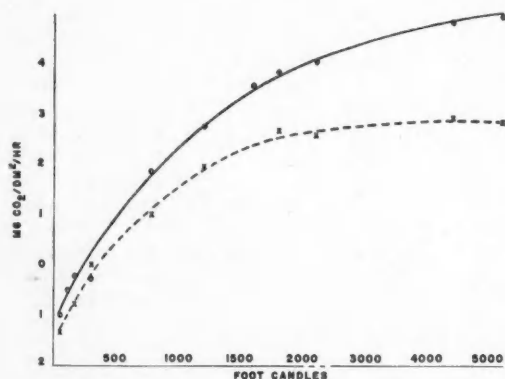


FIG. 17. Photosynthetic light curves at 20°C for a southern alpine population, Loveland Pass, Colorado, and a northern population, Donjek Mts., Yukon Territory. Open circles refer to average photosynthetic rates of plants from Loveland Pass. X's refer to average photosynthetic rates of plants from the Donjek Mts. Note change in light intensity scale between 2,000 and 3,000 fc.

There was little difference in the light compensation points for the two populations. Both were located between intensities of 250 to 350 fc. However, there was a marked difference in the light-saturation figures. The high altitude Loveland Pass population did not become completely light-saturated even at 5,200 fc. On the other hand, the Donjek population attained apparent saturation at approximately 2,000 fc.

FREE AMINO ACIDS, SUGARS, AND PHOTOSYNTHETIC PRODUCTS

Leaves from plants of 4 populations were analyzed for free amino acids, sugars, and photosynthetic products. The leaf material was taken from greenhouse-grown pre-flowering plants in May.

A detached leaf was placed in a photosynthetic chamber with its petiole in a vial of water. The chamber was then sealed and 20% lactic acid was injected into a sidearm of the chamber which contained 50 micro-curies of $\text{NaHC}^{14}\text{O}_3$. After a 5-minute period, during which the leaf was illuminated at the 2,000 fc level, the leaf was extracted in alcohol for several minutes, the alcohol decanted, and an extraction made in boiling water. The supernatants were combined and brought to volume. Aliquots of the extract were chromatographed two-dimensionally with phenol and butanol-propionic acid as solvents. Three chromatograms were made of each sample. One was developed for amino acids with ninhydrin, the second for sugars with anisidine, and the third was used to make a radio-autograph. Activity of the photosynthetic products, as shown by the radio-autograph, was measured and expressed as a percentage of the total activity.

The above procedure was followed for leaves from 2 plants from each of the following populations: Thule, Greenland; Eagle Summit, Alaska; Highwood Pass, Alberta; and Medicine Bow Mts., Wyoming. Table 15 lists the presence of free amino acids and sugars in the leaf samples of the 4 populations.

TABLE 15. Presence of free amino acids and sugars in *Oxyria* leaves

	THULE		EAGLE SUMMIT		HIGHWOOD PASS		MEDICINE BOW	
	a	b	a	b	a	b	a	b
Cysteic acid	+	+	+	+	+	+	+	+
Aspartic acid	+	+	+	+	+	+	+	+
Serine	+	+	+	+	+	+	+	+
Glutamic acid	+	+	+	+	+	+	+	+
Threonine	+	+	+	+	+	+	+	+
Glutamine	+	+	+	+	+	+	+	+
Alanine	+	+	+	+	+	+	+	+
γ -aminobutyric acid	-	-	+	-	+	+	+	+
Leucines	-	-	+	-	+	-	+	-
Proline	-	-	-	-	+	-	-	-
Tryptophane?	-	-	+	+	+	+	+	+
Sucrose	+	+	+	+	+	+	+	+
Fructose	-	-	+	-	+	+	+	+

No pattern was evidenced that distinguished or separated these populations with the possible exception of the relative lack of γ -aminobutyric acid in the arctic populations.

The analysis of the photosynthetic products present in the various populations yielded similar in-

formation. Table 16 lists the products and their percentage activity.

TABLE 16. Photosynthetic products—percent activity

	THULE		EAGLE SUMMIT		HIGHWOOD PASS		MEDICINE BOW	
	a	b	a	b	a	b	a	b
Phosphate area.....	34.3	36.7	34.6	33.2	37.6	30.2	34.9	25.1
Fructose.....	.3	T	.3	.2	T	1.1	1.5	.3
Sucrose.....	16.3	11.7	8.9	17.2	18.1	10.6	12.1	11.4
Maltose.....	.6	.9	.7	.9	—	.5	.8	.6
Glucose.....								
Glycine.....								
Serine.....								
Aspartic acid.....	35.4	39.2	41.5	25.5	22.9	42.3	29.8	29.1
Alanine.....	6.8	4.7	7.0	7.6	14.4	8.2	9.9	13.3
Glutamine.....	T	T	—	.3	1.7	—	.6	.3
Citric acid.....	.8	.5	.7	1.0	1.5	.9	1.0	1.9
Malic acid.....								
Glyceric acid.....	5.4	5.6	6.0	10.2	3.8	6.0	7.0	16.1
Cysteic acid.....	.3	.3	.4	.3	—	.3	.3	.6
Glutamic acid.....	—	—	—	.3	—	—	—	1.3
Glycolic acid.....	—	—	—	.3	—	—	.4	—
Tyrosine.....	—	—	—	—	—	—	.2	—
Leucine.....	—	—	—	—	—	—	.7	—
Sedo-heptulose.....	—	—	—	1.2	—	—	—	—
Lactic acid ?.....	—	—	—	—	—	—	T	—
Unknown.....	—	.4	—	—	—	—	—	—

CARBOHYDRATE AND NITROGEN CONTENTS

FIELD CARBOHYDRATE MEASUREMENTS

The results of the field carbohydrate analyses of *Oxyria* plants in the Medicine Bow Mts. made during the 1958 growing season are plotted in Figure 18. Those given by Russell (1940b) for *Oxyria* on Jan Mayen Island in the Arctic are also plotted. Although his sampling times are not completely comparable to ours, Russell's values are shown in approximate phenological relationship to those from the Medicine Bow alpine area.

Both sets of data are comparable in general aspects; that is, surplus carbohydrate levels were maintained throughout. There was a depletion of carbohydrate reserves during rapid vegetative growth, followed by an increase of stored products. The gradual increase in root starch reserves continued throughout the season.

The primary differences shown by the Jan Mayen series are: (1) depletion of total carbohydrate reserves in the root extended until fruiting, (2) higher carbohydrate levels were attained in the leaves, and (3) of most significance, the amplitude of the root carbohydrate cycle was not nearly as great as that in

the Medicine Bow series. The trend in the latter series is more like the cycles for several other alpine species in the Medicine Bow area (Mooney & Billings 1960). In *Oxyria* and other alpine species in that mountain

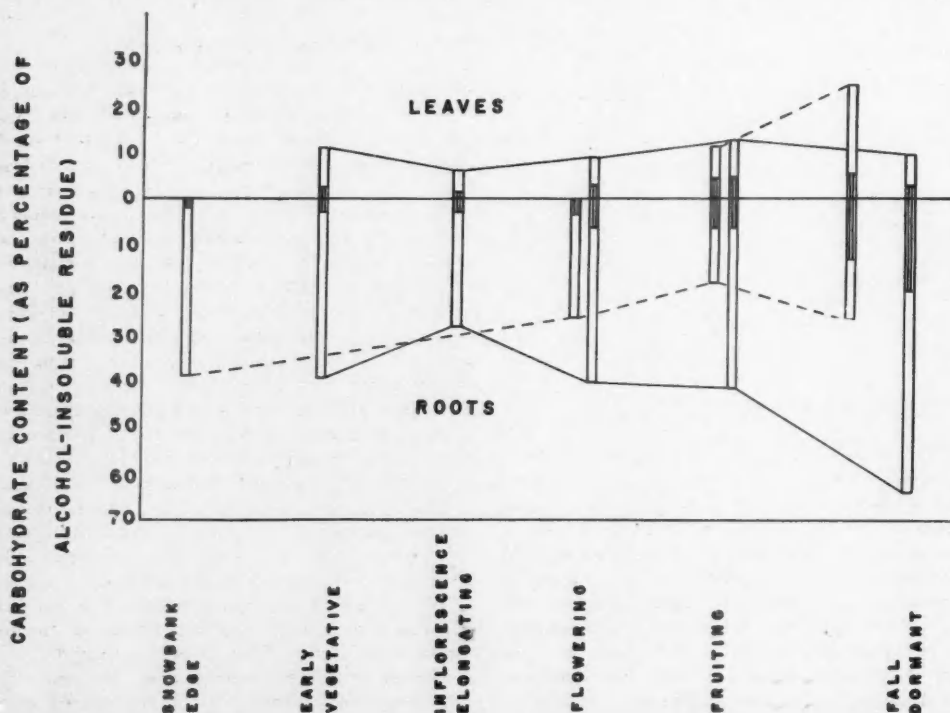


FIG. 18. Seasonal carbohydrate trend in *Oxyria*. Total length of bar indicates total carbohydrate present. Shaded portion represents percent starch. Solid lines connect Medicine Bow Mts., Wyoming values. Dashed lines connect Jan Mayen Island values as determined by Russell (1940b).

range, the depletion of root reserves extended only to the pre-flowering stage. The apparent discrepancy between the root carbohydrate levels at fall dormancy and at early vegetative growth is attributed to respirational loss under the snow. In this instance, the difference may have been partially due to losses during early developmental activities after release from snow but before the first samples were taken.

Samples taken in August, 1958, at Eagle Summit, Alaska, of *Oxyria* in late fruit, yielded mean root carbohydrate values of 28.96% starch, 24.87% total sugar, and 53.50% total carbohydrate, which indicates a carbohydrate cycle of apparently greater amplitude than that of the Jan Mayen arctic series.

FIELD NITROGEN MEASUREMENTS

Mean nitrogen contents of the field samples are given in Table 17 with the phenological stage at the time of collection. In the leaves, and to a lesser extent in the roots, of plants in the Medicine Bow series, there was a definite decrease in total nitrogen in the course of the growing season. The Eagle Summit values were slightly lower than those from the Medicine Bow at a comparable phenological stage. Warren Wilson (unpublished data) found maximum leaf nitrogen values of 4.1% in *Oxyria* plants at mid-season on Jan Mayen Island. There is an indication, then, of possible lower nitrogen content in arctic *Oxyria* plants as compared to alpine forms.

TABLE 17. Seasonal total nitrogen content in *Oxyria* plants*

	Leaves	Roots
Medicine Bow Mts., Wyoming		
Early vegetative.....	6.76	3.26
Inflorescence elongating.....	6.37	2.31
Flowering.....	5.61	1.95
Fruiting.....	5.27	2.30
Fall dormant.....	4.55	2.01
Eagle Summit, Alaska		
Fruiting.....	4.87	1.60

* All values as a percentage of alcohol-insoluble residue.

EFFECTS OF CONTROLLED ENVIRONMENTS ON CARBOHYDRATE AND NITROGEN CONTENTS

Analyses were made of the carbohydrate and nitrogen contents of roots and leaves of plants grown in the arctic and alpine chambers. Composite samples were taken of two plants from each population in each treatment and duplicate determinations were made. Leaf samples were taken from the Elephant's Back, Medicine Bow Mts., Logan Pass, and Sagavanirktok River populations. For root analyses, the northern population, Eagle Summit, was also included. All plants utilized were even-aged fruiting specimens with the exception of those from the two northern populations grown in the alpine chamber.

TABLE 18. Carbohydrate and nitrogen contents of *Oxyria* plants grown in controlled environments*

Population and treatment	Total sugar	Starch	Total Carbohydrate	Nitrogen
<i>Leaves</i>				
Elephant's Back				
Alpine Chamber.	4.52	3.09	7.61	6.01
Arctic Chamber.	7.28	16.95	24.23	5.33
Medicine Bow Mts.				
Alpine Chamber.	3.96	2.03	5.98	7.79
Arctic Chamber.	7.69	5.81	13.50	5.50
Logan Pass				
Alpine Chamber.	5.88	1.07	6.95	7.49
Arctic Chamber.	15.84	14.69	30.53	5.06
Sagavanirktok River				
Alpine Chamber.	2.65	1.56	4.21	6.76
Arctic Chamber.	5.31	3.85	9.16	7.43
<i>Roots</i>				
Elephant's Back				
Alpine Chamber.	21.92	30.08	51.89	1.75
Arctic Chamber.	17.49	41.19	58.68	1.49
Medicine Bow Mts.				
Alpine Chamber.	24.43	36.60	61.01	1.93
Arctic Chamber.	25.04	42.14	67.17	1.12
Logan Pass				
Alpine Chamber.	21.45	17.25	38.70	3.01
Arctic Chamber.	23.74	36.58	60.32	1.33
Eagle Summit				
Alpine Chamber.	8.41	10.01	18.42	4.16
Arctic Chamber.	10.55	45.07	55.62	1.42
Sagavanirktok River				
Alpine Chamber.	5.39	10.29	15.68	3.93
Arctic Chamber.	7.97	34.98	42.95	1.70

* All values as a percentage of alcohol-insoluble residue.

As explained earlier, these did not flower in the alpine treatment because of short photoperiod. The averaged results of these analyses are shown in Table 18.

In the leaves, the percentage of total carbohydrates was two to four times higher in plants from the arctic chamber than in those from the alpine chamber. Compared to the levels in the alpine chamber, there was a much greater increase in total leaf carbohydrate in the alpine populations than in the arctic population when both types were grown in the arctic chamber.

In the roots, the general carbohydrate and nitrogen trend was the same as in the leaves, but there were usually higher values for all carbohydrate fractions. Also, there appears to be a definite geographic trend in the total carbohydrate values. The two southernmost alpine populations had the least spread in values between the two treatments. There was a greater difference in the two values for the delayed-fruited Logan Pass population, and a still greater divergence in the two Alaskan populations. This divergence was a result of the differences in starch values rather than of sugar contents. The root nitrogen values were inversely proportional to the total carbohydrate trend. That is, high carbohydrate corresponded with low nitrogen, and vice-versa. Low C/N ratios were characteristic of the delayed or non-fruited samples.

Analyses of soils taken from the pots of plants grown in the arctic and alpine chambers showed little,

if any, variation in nitrogen content. The values were, respectively, 0.16 and 0.15% of dry weight. Hence, the different nitrogen contents of the plants from these chambers must have been a result of climatic differences between their environments, rather than the result of soil differences.

CARBOHYDRATE AND NITROGEN CONTENTS OF GREENHOUSE-GROWN PLANTS

Carbohydrate and nitrogen analyses were made on plants transplanted from the field to the greenhouse. These plants were brought into flower by using a 24-hr photoperiod. Samples were taken at the end of March when all were in fruiting condition except the Eagle Summit, Alaska, specimens which had aborted inflorescences. In addition to the Alaskan population, samples were taken from 4 southern alpine populations: Elephant's Back, Loveland Pass, Niwot Ridge, and Beartooth Mts. The results of these analyses are given in Table 19.

TABLE 19. Carbohydrate and nitrogen contents of greenhouse-grown plants*

	Total sugar	Starch	Total Carbohy- drate	Nitrogen
<i>Leaves</i>				
Elephant's Back.....	1.71	0.90	2.61	7.38
Loveland Pass.....	5.64	3.87	9.51	7.98
Niwot Ridge.....	6.71	1.99	8.70	8.30
Beartooth Mts.....	4.36	1.92	6.28	7.13
Eagle Summit.....	1.56	1.82	3.37	7.57
<i>Roots</i>				
Elephant's Back....	6.98	21.51	28.48	2.77
Loveland Pass.....	24.97	6.42	31.39	2.13
Niwot Ridge.....	9.04	3.12	12.12	2.67
Beartooth Mts.....	16.20	3.42	19.63	2.78
Eagle Summit.....	4.98	20.29	25.27	3.92

* All values as a percentage of alcohol-insoluble residue.

There was considerable variation in values in both the leaves and the roots. This variation may be indicative of a nutritional imbalance which did not become fully apparent until two months after the sampling date when large numbers of *Oxyria* plants began to die, apparently due to high summer temperatures.

If only fruiting plants are considered, the four alpine populations of the greenhouse series may be compared only with the arctic chamber series or with the Elephant's Back or Medicine Bow populations in the alpine chamber. In making this comparison, the most striking difference is in the low level of root carbohydrate reserves in the greenhouse-grown plants. This suggests either a large depletion of such reserves or that high reserve levels were never attained under the relatively high temperatures of the greenhouse.

COMPARISON OF FIELD AND LABORATORY RESULTS

Carbohydrate and nitrogen contents of mountain-grown fruiting *Oxyria* plants from the Medicine Bow

Mts. were compared with results of similar analyses of fruiting plants of the same population grown in the alpine chamber. An analogous comparison was made between fruiting plants of the Eagle Summit population from the field and from the arctic chamber. The results of these comparisons are listed in Table 20.

TABLE 20. Comparison of field and laboratory carbohydrate and nitrogen contents*

	Total sugar	Starch	Total Carbohy- drate	Nitrogen
<i>Medicine Bow Mts.</i>				
<i>Leaves</i>				
Field.....	7.35	5.90	13.25	5.27
Laboratory..	3.96	2.03	5.98	7.79
<i>Roots</i>				
Field.....	35.38	5.66	41.04	2.30
Laboratory..	24.43	36.60	61.01	1.93
<i>Eagle Summit</i>				
<i>Roots</i>				
Field.....	24.87	28.96	53.50	1.60
Laboratory..	10.55	45.07	55.62	1.42

* All values as a percentage of alcohol-insoluble residue.

The total carbohydrate content in the roots of the cultivated plants was either similar to or in excess of that in field-grown plants. This is evidence that the cultivated plants were not operating at a carbohydrate deficit. Furthermore, the conditions of the laboratory enabled the plants to maintain the high carbohydrate reserve which is characteristic of many arctic and alpine species in the field (Russell 1940b, Mooney & Billings 1960).

The root nitrogen content of plants grown in the field was slightly higher than the root nitrogen of those plants grown in the laboratory. The reverse was true of leaf nitrogen contents. Environment apparently has a strong influence on the nitrogen balance of *Oxyria*, as has been shown earlier in the comparison of analyses of plants grown in the arctic and alpine chambers.

HIGH TEMPERATURE TOLERANCE

During the warmest part of the summer of 1959 in Durham, North Carolina (latitude 36° N), several hundred greenhouse-grown *Oxyria* plants died. It is significant that the high death rate in *Oxyria* occurred during a period when populations of other arctic-alpine species (*Poa alpina*, *Silene acaulis*, and *Trisetum spicatum*), growing under the same conditions, though affected, were not killed in large numbers. From June through August, the weekly maxima in the greenhouse ranged from 35° C to 43° C. During July and August, the greenhouse temperature never fell below 21° C.

The percentage of total population dead at given time intervals during the summer is plotted in Figure 19 for two northern and two southern populations of *Oxyria*. These results appear to indicate a difference

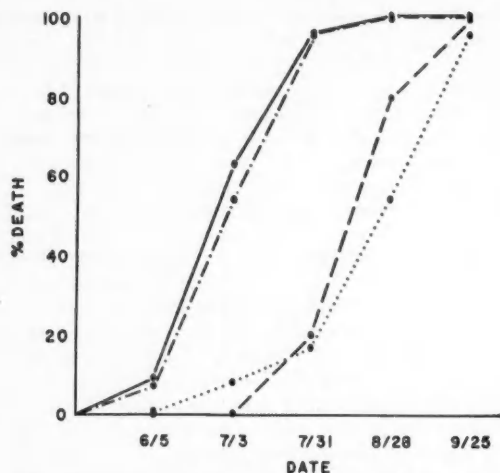


FIG. 19. Summer death rate of plants of two northern and two southern *Oxyria* populations under greenhouse conditions in Durham, North Carolina. — Donjek Mts., Yukon Territory, - - - Pitmegea River, Alaska, — — — Medicine Bow Mts., Wyoming, Logan Pass, Montana.

in tolerance to high temperatures between northern and southern populations. An experiment was designed to evaluate these apparent differences.

Seedlings of a southern population, Logan Pass, Montana, and a northern population, Donjek Mts., Yukon, were germinated in sand and grown at a constant 20° C under 24-hr light. After 2 weeks, the seedlings were individually washed free of sand and transferred to green vials containing complete Hoagland's solution. Each plant was held in place by a paraffined split cork and cotton. For 10 days the young plants were kept at a constant 20° C to become established. Then they were placed for 12 hrs alternately in a dark incubator at 40° C and in a lighted constant temperature room at 20° C. Daily observations were made on 10 plants from each population. These were scored for percentage of plants with all leaves wilted, and percentage of plants with all leaves dried. The results of this experiment are

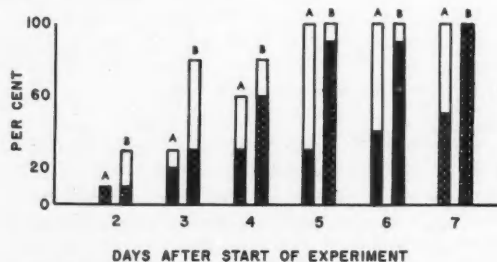


FIG. 20. Experimental heat tolerance. A, Logan Pass population, B, Donjek Mts. population. Shaded areas, plants with all leaves dried; unshaded areas, plants with all leaves wilted.

presented in Figure 20. These data indicate that plants from the southern population had a decidedly greater tolerance of high temperature in the dark than did those from the northern source.

DISCUSSION

The primary objective of this research was to determine how *Oxyria digyna* is able to grow successfully in such a wide array of severe habitats, ranging from the northern arctic tundra to southern alpine locations. We now have some information which may help to explain this wide distribution. For example, when different geographic populations of *Oxyria* are grown together under uniform conditions, morphological and physiological differences between the populations become readily apparent. Many of these differential characteristics appear to be of direct adaptive significance in either arctic or alpine environments and thus can be considered as ecotypic modifications. The question now becomes, "How are these ecotypes related to their respective environments?" The following discussion will attempt to answer this question, at least partially, by examining each of the principal kinds of modifications.

RHIZOME FORMATION

The presence of vegetative reproduction in arctic *Oxyria* plants has been reported for Alaska (Wiggins 1951), the Canadian East Arctic (Gelting 1934, Holm 1922, Savile 1959), and Greenland (Sørensen 1941). Our results indicate that rhizome formation is genetically controlled. Only plants of the northern populations produce rhizomes.

Two possible explanations may be offered as to why rhizome production is important in northern habitats but not in southern alpine locations. First, rhizome production may have survival value in the unstable substrates of the northern habitats where vegetative reproduction could be of competitive advantage. Disturbed habitats resulting from soil movement may be revegetated more rapidly by rhizomes or rhizome fragments than by plants from seed. This possibility has been discussed by Wiggins (1951). Secondly, it has been shown here that seed production is reduced in the northern *Oxyria* populations. Vegetative reproduction may compensate for this reduction and insure survival of the species even though there may be unfavorable periods for flowering and seedling development.

ADAPTATIONS TO LIGHT

The light climates of arctic and alpine habitats differ considerably from each other. They vary not only in duration but also in intensity and equality of light. It appears that any given *Oxyria* population is well-adjusted to the specific light climate of its habitat through adaptations in growth and flowering response, perennating bud formation, leaf chlorophyll content, and photosynthetic light saturation.

Definite growth responses to different photoperiods have been shown for *Oxyria* populations in the present study. Under a 15-hr photoperiod, maximum growth was observed in populations originating from a region where the maximum natural day-length is 15 hrs. The further north the geographic origin of the population, the smaller was the amount of vegetative growth made under short photoperiod.

Related to the clinal growth response of *Oxyria* populations is a similar cline of flowering response. The latitudinal populations have variable photoperiodic requirements for flowering which agree closely to the maximum photoperiod of their natural habitat. However, a given geographic population appears to have some members whose physiological responses are like those of adjacent geographic populations, thus giving ecological amplitude to the population. These slightly different biotypes could allow limited north-south migrations with changing climates. It would appear easier, because of minimum photoperiodic requirements, for migration to take place from south to north, rather than the reverse.

Population differences in photoperiodic requirement for flowering are of considerable ecological significance. The maximum photoperiod in any arctic or alpine habitat coincides with the onset of favorable temperatures for growth. Late snowbed plants even though released at a period later than June 21 receive their maximum photoperiod at the beginning of their growth period.

Photoperiod is also important in the stimulation of the formation of perennating buds in *Oxyria*. A photoperiod below that necessary for flowering results in the formation of a perennating bud. Although the populations were not scored for critical thresholds, it was established that a 12-hr photoperiod causes all of our populations to form perennating buds even at relatively high temperatures. It would appear then, that toward the termination of the growing season, perennating buds would be formed under the stimulation of the decreasing photoperiod in the natural habitat. It would not be surprising if the differences in photoperiodic requirement for perennating bud formation were more nearly the same for the various latitudinal populations than are the photoperiodic requirements for growth and flowering. The difference in length of photoperiod between a southern alpine habitat and an arctic one is greatest at the beginning of the growing season and becomes much less toward the end and, of course, the difference becomes zero for a short period in September.

Quantitative differences in the photoperiodic requirement for breaking dormancy were not determined. It was established, though, that under the influence of a 24-hr photoperiod, dormancy was broken in all populations unless subfreezing temperatures prevailed.

It appears, then, that in *Oxyria*, the whole series of events from the breaking of dormancy, through

flowering, and to the formation of perennating buds is strongly under the influence of photoperiod, subject to modification by temperature. Quantitative differences, between the populations, in photoperiodic requirement for growth and flowering have been demonstrated; they probably exist also for perennating bud formation.

Differential phenological response of a series of latitudinal races to photoperiod has been shown for several kinds of plants (Olmsted 1944, Larsen 1947, McMillan 1959, Vaartaja 1954, 1959) and is probably a common, but not universal, phenomenon in widely distributed species.

There is also some evidence that there is ecotypic variation in *Oxyria* in response to the light intensity of the environment. The photosynthetic light curves which were plotted at a constant temperature for a northern population and a southern population of *Oxyria* show that the latter or high altitude population approaches photosynthetic light saturation at a much higher light intensity than does the northern or low altitude population.

The latitudinal cline in chlorophyll content may be related to these differences in photosynthetic light saturation. Low latitude, high elevation populations have a lower chlorophyll content than the high latitude, low elevation populations. A similar latitudinal cline in chlorophyll content is known for races of *Pinus sylvestris* (Gerhold 1959).

There is, perhaps, additional adaptive significance to the differences in chlorophyll contents of the various populations. Reduced chlorophyll content in leaves of alpine populations would result in less visible light absorption and perhaps a more favorable energy balance. Billings & Morris (1951), for example, found that in plants from high light intensity environments there was greater reflectance from the leaves than occurred from leaves of plants growing in shaded habitats.

ADAPTATION TO TEMPERATURE

Northern *Oxyria* populations show characteristics which indicate that they are adapted to lower temperatures during the growing season than southern populations. They appear to carry on photosynthesis at a higher rate at lower temperatures and, furthermore, attain their maximum rate at a lower temperature. Also, in contrast to the situation in southern *Oxyria* populations, the respiration rate increase with temperature in northern populations is more rapid and the rate is higher at all temperatures.

Beljakoff (1930) found similar photosynthetic differences in two morphologically distinct races of barley. A northern race, "Vegakorn," cultivated in Sweden from 62° to 66° N latitude, was found to have a temperature optimum for photosynthesis of 20° C. A second race, "Gullkorn," is grown from 62° N southward. The latter race was found to have a temperature optimum for photosynthesis 10° C higher than that of "Vegakorn."

The higher respiration rate may enable plants of a northern *Oxyria* population to develop as rapidly in the colder arctic environment as do plants of a southern population at higher temperatures. Such a respiratory temperature compensation has been investigated by Scholander & Kanwisher (1959) in northern and southern populations of nine sub-arctic plant species. They found significantly higher respiration rates in northern populations of two of the species, *Lycopodium annotinum* and *Equisetum sylvaticum*.

Pisek & Winkler (1958) indicate that there may be an altitudinal cline in the respiration rate of *Picea excelsa* similar to the latitudinal cline in *Oxyria*. They found considerably higher respiration rates in spruce during the summer at timberline at 1,840 m than in trees of the same species in a botanic garden at 600 m or in lowland spruce forests at 580 m.

Our evidence indicates that the southern *Oxyria* populations are more tolerant of high temperatures than are the northern *Oxyria* populations. They were more resistant to abnormally high summer temperatures and to experimentally controlled high temperatures. This higher temperature tolerance may be related to the higher temperature compensation points of plants of the southern populations. Such characteristics in southern populations would tend to conserve high carbohydrate reserves which are of considerable importance to the survival and rapid growth of arctic-alpine plants.

In general, the characters measured on the mass collections and on the chamber- and greenhouse-grown plants indicate a northern and a southern morphological population group. The Highwood Pass population from Alberta is aligned in some characteristics with the southern group and in other characteristics with the northern group. In other characteristics, it is intermediate. There are also physiological differences associated with these two population groups.

The approximate boundary between the northern and southern population groups coincides geographically with the extent of maximum Pleistocene glaciation. At present, most areas which were covered by continental glaciation are occupied by populations with apparent northern affinities. The morphological and physiological differentiation between the northern and southern population groups may have been accentuated by separation of the two groups by continental ice during the Pleistocene. It would appear that recolonization of the continentally-glaciated northern Cordilleran region was almost entirely by photoperiod-tolerant biotypes from arctic populations. On the other hand, the alpine populations of the central and southern Rocky Mountains and the Sierra Nevada seem not to have migrated very far north into Canada. These populations may have been confined to these southerly mountain ranges by post-Wisconsin aridity barriers.

Although *Oxyria* apparently is composed of ecological races which react differently to environmental

influences, the overall responses of plants from several populations make possible some inferences concerning the tolerances of an arctic-alpine species. The primary restrictive factor limiting the distribution of *Oxyria* appears to be relatively high summer temperature. The low photosynthetic economy of plants of this species at high temperatures causes a depletion of carbohydrate reserves. This depletion, perhaps coupled with malfunction of certain enzyme-substrate systems, results in consequent death. The results of Müller (1928) on arctic plants and Dahl (1951) on alpine plants support this hypothesis that high summer temperature determines to a large degree the southern or lower altitudinal limits of a tundra species.

SUMMARY

1. A comparative study was made of the morphological and physiological variation between geographically-separated populations of *Oxyria digyna*, a widely distributed arctic-alpine species. A latitudinal series of North American populations was studied ranging in origin from Colorado and California to Thule, Greenland, and Pt. Barrow, Alaska. The habitat and associates of each population are described.

2. Analysis of mass collections and plants grown under controlled conditions indicate two primary morphological groups within the range studied. One morphological group encompasses all the populations from southern Alberta southward in an area largely to the south of maximum Pleistocene continental glaciation. The other group includes all of the northern populations. The major morphological differences between these groups are in stamen number, inflorescence branch number, and presence or absence of rhizomes.

3. Measurements of field photosynthesis and the seasonal carbohydrate cycle of a Wyoming alpine population were compared with published results of these processes in arctic populations. Comparable photosynthetic rates were found, although the amplitude of the alpine carbohydrate cycle was greater than in the arctic plants.

4. A series of arctic and alpine populations was grown in controlled environment chambers which simulated either alpine growing conditions at 41° N latitude or arctic growing conditions at 71° N. The growth and development, photosynthesis and respiration rates, leaf chlorophyll contents, and leaf and root carbohydrate and nitrogen contents were measured on plants of these populations.

5. In these "arctic" and "alpine" conditions, it was found that photosynthetic rate, and chlorophyll and nitrogen contents were depressed while carbohydrate content was generally increased in plants of most populations under arctic treatment. In the arctic chamber, all plants flowered. In the alpine chamber, there was a cline in growth rate from a maximum rate in the southern populations to a minimum in the far northern populations. Flowering of all plants

in a population occurred in only those populations which received a photoperiod corresponding to the maximum photoperiod of their natural habitats.

6. A comparison of the physiological responses between populations when grown under suitable conditions for flowering showed the following:

a. There is a north to south cline of increased flower production. From south to north, there is increased rhizome production.

b. Leaf chlorophyll content increases with latitude.

c. Plants of northern populations have a higher photosynthetic rate at lower temperatures and attain the maximum rate at lower temperatures than do plants of the southern alpine populations.

d. Plants of northern populations have higher respiration rates at all temperatures than do plants of southern alpine populations.

e. High elevation, low latitude plants attain photosynthetic light saturation at a higher light intensity than do low elevation, high latitude plants.

7. The response of the various populations to photoperiod is reflected in their latitudinal origin. There was a clinal increase in photoperiodic requirement for flowering from the southern to northern populations. Formation of perennating buds was also found to be under photoperiodic control.

8. Although all populations were found to be intolerant of abnormally high summer night temperatures, the southern alpine populations displayed a somewhat greater tolerance than did the northern ones.

9. From these results, it is concluded that the continued existence of *Oxyria digyna* throughout a wide range of arctic and alpine conditions is due in large part to differences in metabolic potential among its component populations.

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RELATIONSHIPS BETWEEN PLANT LIFE-FORMS AND MICROCLIMATE IN SOUTHEASTERN MICHIGAN

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INTRODUCTION

Raunkiaer's well known system of plant life-form classification shows relationships between relative importance of certain life-form classes and major world climatic zones. Recent investigations have shown that there are also differences in life-form distribution related to climatic variations within the larger "phytoclimates." Several reviews (Adamson 1939; Cain 1950; Cain & Castro 1959) have summarized our understanding of these life-form concepts.

Relationships between life-forms and microclimate, however, have not been intensively investigated. Cain (1950) suggests that "Although life-form spectra have been employed mostly for general climatic analysis, there are enough studies available to suggest that they may be even more useful for the analysis of climatic variants and microclimates." The limited data available in the literature provide enough evidence that life-form distribution varies with differences in topography and microclimate to warrant further investigation of the subject.

The possible indicator significance of variations in community life-form composition also have received little attention. Whittaker (1954) points out that "composition of vegetation in terms of life-forms and growth-forms may indicate position along local gradients." Furthermore, the fact that a plant's life-form represents, in theory, a fundamental adaptation to environment makes community life-form composition of greater potential value than community species composition for use as an indicator of site (microenvironmental) conditions.

This study was an intensive investigation of the vegetation and microclimates of north- and south-facing (henceforth referred to as north and south) slopes on the E. S. George Reserve in southeastern Michigan. The data obtained were used to demonstrate relationships between Raunkiaerian life-forms and microclimate and to illustrate the value of community life-form data as indicators of habitat conditions.

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REVIEW OF THE LITERATURE

Physiognomy has long been an important feature in the description and analysis of vegetation. Early physiognomic systems were primarily descriptive and did not attempt to express environmental relationships. However, under the influence of Darwin's ideas, systems developed which sought not only to be descriptive but also to express relationships between physiognomic characters of the plant and

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its environment (DuRietz 1932). Warming's (1884) "biological life-form system" was the first of a series which culminated with publication of Raunkiaer's life-form system in 1904.

Cain (1950) has reviewed the bases of life-form systems and has pointed out that such systems have no relation to phylogenetic systems of classification but are based on the architecture or structural adaptations of the plant. However, phylogenetic considerations cannot be removed entirely for certain groups may be hereditarily disposed toward a certain life-form (Cain 1950). Numata & Asano (1956) point out such a case in the abundance of geophytes among monocots.

Of the many life-form systems only that of Raunkiaer has achieved any degree of universal acceptance (DuRietz 1932). This classification, originally limited to flowering plants, was based on the degree of protection afforded the perennating tissue during the unfavorable season. Five classes, each with subdivisions, were established: 1) *Phanerophytes* (buds 25 cm or more above the substratum); 2) *Chamaephytes* (buds in the first 25 cm above the soil surface); 3) *Hemicryptophytes* (buds at or in the soil surface); 4) *Cryptophytes* (buds hidden under the soil or in muck or under water); 5) *Therophytes* (annuals). The entire classification, with subdivisions, is discussed in Cain & Castro (1959).

Raunkiaer's system has been used widely in floristic (Ennis 1928; McDonald 1937) and vegetational studies. Raunkiaer himself presented the first vegetational analyses. Using a "normal spectrum", showing the percent representation of each life-form in the world flora, as a standard, Raunkiaer showed that there were four main phytoclimates each characterized by an increase in the percentage of a life-form over its percentage in the "normal spectrum." These were: a *Phanerophytic* climate of the warm, humid tropics; a *Therophytic* climate of warm, arid desert regions; a *Hemicryptophytic* climate of middle latitude deciduous and coniferous forest regions; and a *Chamaephytic* climate of cold areas.

Numerous other vegetational studies have supported and amplified Raunkiaer's conclusions. These have been reviewed in detail (Adamson 1939; Cain 1950; Cain & Castro 1959).

Recent studies have shown variations in community life-form composition related to climatic gradients. Buell & Wilbur (1948) and Buell & Cantlon (1951) showed an increase in the importance of protected life-forms in forest stands along the prairie border in Minnesota as opposed to forest stands further east. This trend appeared to be related to climatic data showing the prairie border to have a colder, drier climate than the area to the east. Stern & Buell (1951) found an increase in chamaephytes, hemicryptophytes, and cryptophytes and a decrease in phanerophytes from the shortleaf pine communities of the New Jersey pine barrens to the jack pine communities of Minnesota, and suggested this trend was related to differences in climate between the mild

Atlantic coastal plain and the more severe climate of Minnesota. Archard & Buell (1954) found a similar trend when comparing oak-pitch pine communities in southern and northern New Jersey. Cain *et al.* (1956) found that in Brazilian rain forest phanerophytes dominated to the virtual exclusion of other life-forms. As stands southward from the equator were sampled, phanerophytes diminished and there was a trend toward the hemicryptophyte dominance characteristic of temperate areas.

Several studies provide limited data on relationships between life-forms and the presumed or documented microclimates of north- and south-facing slopes in deciduous forest areas (Table 1). From the data it appears that phanerophytes and cryptophytes are more numerous on north-facing slopes whereas hemicryptophytes and therophytes predominate on south-facing slopes. The large number of cryptophytes on the north-facing bluff in North Carolina suggested a cryptophyte climate to Oosting (1942) (although no such category has yet been suggested) and he posed the question as to whether cryptophytes might regularly reach this degree of importance in such topographic situations in hemicryptophytic climatic areas. Miller & Buell's (1956) results deserve further comment. Although the presence spectra cited in Table 1 agree with other spectra, quantitatively-based spectra showed a greater proportion of cryptophytes on the southwest-facing slope.

TABLE 1. Presence-based life-form spectra from north- and south-facing slopes in eastern American deciduous forest.

Location	No. of Species	Ph	Ch	H	Cr	Th	Author
<i>Piedmont, N. C.</i>							
South-facing bluff.....	45	26.6	0.0	51.1	4.4	17.8	Oosting, 1942
North-facing bluff.....	84	45.2	3.6	25.0	27.4	0.0	
<i>Cushetunk Mt., N. J.</i>							
South-facing slope.....	112	32.1	1.8	46.4	12.5	7.1	Cantlon, 1953
North-facing slope.....	86	41.8	1.2	41.8	15.2	0.0	
<i>Itasca Park, Minn.</i>							
Southwest-facing slope....	50	25.0	2.0	55.0	18.0	0.0	Miller & Buell, 1956
Northeast-facing slope....	62	41.0	3.0	33.0	23.0	0.0	
<i>Southeastern Michigan</i>							
South-facing slope.....	94	25.5	2.1	57.5	8.5	6.4	Cooper, Prelim. invest.
North-facing slope.....	89	35.9	1.1	49.5	13.5	0.0	

Failure of the usual life-form spectrum to take into account the importance of plants in the community has long been recognized (Taylor 1918; Cain 1945). Quantitatively-based spectra, using density (Buell & Cantlon 1951), frequency (Cain 1945; Buell & Wilbur 1948), and coverage (Stern & Buell 1951; Archard & Buell 1954; Miller & Buell 1956) have been used to show variations in community life-form composition. Of these measures coverage seems the most promising (Cain & Castro 1959).

Leaf-size, an aspect of life-form, has also been utilized in vegetational analysis. Botanists have long been aware that, in general, leaf sizes of plants be-

come smaller the more unfavorable (dry or cold) the environment. Raunkiaer (1916) was the first to make use of this generalization as an ecological tool. In formulating his leaf-size concept, Raunkiaer reflected the prevalent ideas of his day which assigned primary importance to relations between plants and their water supply. Many structural features such as covering of wax, thick cuticle, water storage tissue, and diminution of transpiring surface were assumed to enable plants to endure conditions causing excessive evaporation. Of these, leaf surface area best lent itself to statistical treatment. After examination of a large sample of the world flora, Raunkiaer enumerated seven leaf-size classes with limits set at points in the range of leaf sizes where natural limits seemed to fall. These were: *Aphyll* (leafless); *Leptophyll* ($<25 \text{ mm}^2$); *Nanophyll* ($<225 \text{ mm}^2$); *Microphyll* ($<2025 \text{ mm}^2$); *Mesophyll* ($<18225 \text{ mm}^2$); *Macrophyll* ($<164025 \text{ mm}^2$); *Megaphyll* ($>164025 \text{ mm}^2$).

Certain problems have limited the use of leaf-size data in vegetational analysis. Thoday (1931) objected to the idea that small leaves are an adaptation to extreme environments because in some plants large numbers of small leaves are the equivalent of small numbers of large leaves, resulting in no decrease in transpiring surface. Actually, transpiration per unit area may be increased as there is no interference by vapor layers over the numerous small leaves. Difficulties involved in determining area have also limited the use of leaf-size classes. Recently, Cain *et al.* (1956) showed that leaf areas determined by multiplying the product of leaf length and width by $2/3$ introduced no real error in determination of leaf-size class in tropical species. This procedure was used in the present study (Cooper 1960b).

Vegetation studies using leaf-size data are not numerous. Withrow (1932) found upland and climax forests in the Cincinnati area were characterized by leaves of mesophyll size but that there were more microphylls in the upland forest than in the climax. Grassland, arid, and hydrophytic communities in the same area were predominantly microphyllous and she concluded that "with an increase in xerophytism there is a decrease in the percentage of large leaf-size classes and an increase in the smaller ones." Cuatrecasas (1934 in Dansereau, 1957) showed that in Colombia leaf size was greatly affected by altitude, no nanophylls being found below 3600 m and no macrophylls above this limit. Cannon (1921) found that there were no plants in arid south Australia with leaves larger than 1951 mm^2 and 90% had either nanophylls or microphylls. Cain *et al.* (1956) showed that in tropical rain forest there was a general decrease in leaf size with increasing distance from the equator. In true rain forest at the equator 68% of all species had mesophylls whereas further south in gallery rain forest only 24% of leaves were mesophylls and microphylls had increased to 54%.

No review of the extensive literature dealing with microclimates will be attempted as recent comprehen-

sive reviews, at least up to the early 1950's, are available (Baum 1948, Wolfe *et al.* 1949; Cantlon 1953; Geiger 1957). However, as this study deals with the inter-related effects of topography and forest vegetation on microclimate and the role of microclimate in determining vegetational differences, one point must be made. Geiger (1957) has stressed the importance of the canopy to climatic conditions within the forest. As the upper surface of the canopy is the region where radiation interception occurs, it is thus impossible to compare the climate of an open area with that of the forest trunk space, because the "trunk space climate" is a result of an entirely different set of meteorological circumstances. Thus, the "trunk space area" of the forest is a distinctive microclimate. As will be shown, the data of the present study suggest some changes in the typical "trunk space climate" which topographic variations may produce.

THE STUDY AREA

The E. S. George Reserve, the site of this study, is located approximately 4.5 mi west of Pinekey and 23 mi northwest of Ann Arbor, in south-central Livingston County, Michigan. The Reserve is slightly less than 2 sq mi in area and has been fenced since 1928. The rugged glacial topography and the protection afforded instruments make the area ideal for microclimatic study. This study was confined to the Big Woods, the largest tract of woodland on the Reserve.

PHYSIOGRAPHY

The area is one of rolling glacial outwash topography, the primary land forms having originated during retreat of the Saginaw and/or Lake Erie lobes of the Cary substage of the Wisconsin glaciation. The topographic features of the Reserve uplands were probably formed during a period of rapid deterioration of the ice sheet as the esker- or kame-like formations, the large outwash plain, the numerous kettle holes, and the predominantly sandy texture of the soils suggest. Elevations vary from about 880 ft above sea level in the marshes of the southeastern portion to over 990 ft at several locations in the Big Woods. Local relief may exceed 80 ft, particularly along the sides of the main esker in the Big Woods. Due to the sandy soil, drainage of the uplands is good. In areas of pronounced local relief it may be excessive.

VEGETATION AND LAND-USE HISTORY

The pre-settlement forest of southwestern Livingston County, including the Reserve, appears to have been similar in species composition to that of today. Oaks, predominantly black and white, and hickories were the trees cited most frequently by the team which surveyed the area in 1825. "Prairie" (a term apparently used for grass-dominated lowlands), marsh, and tamarack swamp were mapped as occupying lowland sites much as they do today.

The original vegetation of the Reserve has been greatly altered by man. Logging, agriculture, graz-

ing, and fire have dissected the upland forest and all that remain are isolated, more or less altered, stands. Present vegetation of the Reserve consists of approximately equal parts marsh and swamp, old fields, and second growth oak and oak-hickory woodland. Marshes and swamps occur slightly above and below the 900 ft contour. The old fields, now dominated by blue-grasses (*Poa compressa* L., *P. pratensis* L.) and forbs, are confined chiefly to the level uplands. The woodlands generally occupy uplands which, because of their irregular topography, were unsuitable for agriculture.

There is no actual written history of the Reserve, but Cantrall (1943) found that most of the farmlands now included in the Reserve were cleared by 1870. The presence and age of old-growth species such as sassafras and bigtooth aspen, in addition to the sprout origin of many oaks, indicate that extensive logging took place in the period 1860-1900. Also, all of the woodlands were heavily grazed during the period of farming. After 1900 agriculture gradually diminished and the land was virtually abandoned by 1926 when it came into the possession of the late E. S. George. Administration has been by the University of Michigan since 1933. Since that time the fence has minimized human disturbance, and no fire, lumbering, or cultivation has taken place. However, a deer herd has been maintained on the Reserve and the magnitude of the browsing effects of the deer is a debatable question. There is no doubt that in the past they have retarded return of forest to the open fields (Evans & Cain 1952), but since the herd was cut to 25 animals per square mile in the early 1950's succession seems to have accelerated.

SOILS

The upland soils of the Reserve are gray-brown podzolics and show horizon development characteristic for this great soil group. Parent materials are predominantly coarse-textured glacial outwash. Being water-laid deposits, parent materials are commonly bedded and may include lenses of gravel, sand, and even silt and clay. The soils are classified for the most part as sandy loams, loamy sands, or sands. The Livingston County soil survey (Wheeting & Bergquist 1923) shows the greater part of the upland soils of the Reserve to be Bellefontaine sandy loam with small areas of Miami loam in the southern portion. The poorly-drained soils, generally below the 900 ft contour, are either Carlisle muck, Greenwood peat, or Rife peat.

Veatch (1953) described a number of soil types in the Big Woods ranging in texture from a fine sandy loam to a sand. The great diversity in soil units is due in part to the heterogeneous glacio-fluvial parent material and in part to the numerous topographic irregularities of the area. For example, Cooper (1960a) has shown that the differences in the microclimates of the north and south slopes appear to be major factors in producing different profiles of weathering on these slopes. Soils with more

silt and clay in the B horizon, the Bellefontaine series, are found on south slopes, whereas more weakly-developed profiles, possibly to be classified as Coloma or Plainfield, are formed on many north slopes.

REGIONAL CLIMATE

The climate of southeastern Michigan is typical of humid, microthermal regions and is of the Koepfen Dbf type. There is a well-defined winter with considerable snow alternating with an equally well-defined summer. Spring and fall are generally short in duration. Precipitation is well-distributed throughout the year; summer, however, is usually the season of maximum rainfall.

No records of solar radiation are taken on the Reserve. However, data for East Lansing, Mich., approximately 40 mi to the northwest, are available (Crabb 1950; U. S. Dept. of Commerce 1957). The smoothed annual curve for East Lansing (Crabb 1950) is lower than comparable curves for most other U. S. stations. Crabb suggests this is due to the large amounts of moisture contributed to the atmosphere by the surrounding Great Lakes. Furthermore, the annual curve shows a spring plateau, related to moisture added to the atmosphere by the freshly ice-free Great Lakes, and twin summer peaks (Crabb 1950). During 1957 there were two spring plateaus (March 12–April 9 and April 23–May 14) and the second summer peak was the higher, rather than the first as is usual.

An 8-yr record of local temperature and rainfall is provided by a weather station located on the Reserve. The average annual temperature, as indicated by data from this station, is 46.9° F. (All temperatures henceforth referred to are in °F). The average maximum is 56.8° and the average minimum 37.1°. January (23.6°) and February (25.5°) are the coldest months and annual lows are usually recorded in either of these months. The 8-yr low, -3.5°, occurred in February, 1958, after this study was concluded. July has the highest average temperature (70.7°), although the annual high may occur anytime during June–September. The all-time high is 97.8°.

The average annual temperature during 1957 was 46.0°, the average maximum temperature was 55.9°, and the average minimum temperature was 36.2°. The similarity between these values and the 8-yr means indicated that 1957 was a year with no major temperature irregularities. However, January was the coldest month on record, with lows for all temperature records up to that time being recorded.

Several features of the annual march of temperature during 1957 are significant. The annual low (-6.5°) occurred during the third week of January. The two weeks with the greatest temperature range, March 10-16 (53.5°) and April 14-20 (53.7°) coincided with the weeks during which early spring and late spring (see page 35) began. A plateau in the curve during the weeks of March 24–April 14 marked

an extended period of wintery weather interrupting the progress of spring. A rapid climb from April 14 to May 5 marked the advent of the growing season, but a plateau in this upward trend was caused by the annual cold rainy spell of mid-May. Both spring temperature plateaus were closely related to the corresponding plateaus in solar radiation. Another period of cool, rainy weather in late June and early July caused a recession in the steady rise of temperature to the annual July maximum.

Total annual precipitation averages 33.7 in. Perhaps slightly more falls during summer than in other seasons. With one exception no major differences between long-term precipitation patterns and those of 1957 occurred. July, however, was extremely wet, with most of the record July rainfall (5.1 in.) falling in the first 13 days of the month. Extended summer droughts, which often do not appear in monthly rainfall data, are an annual occurrence. Dry periods (with less than 0.1 in. of rain) of 22 days (July 24-August 14) and 24 days (September 23-October 16) occurred in the summer and fall of 1957.

Annual snowfall averages 41.5 in. and ranges from 26 to 53 in. The average total is evenly spread over the period from December 1-March 31, but in a given year heavy snow may occur in any of these months. Snowfall during 1956-57 was about 6 in. below average. However, the January total of 13.4 in. was the heaviest ever recorded for that month.

THE SEASONS ON THE GEORGE RESERVE

An important aspect of the climate of an area is the character and duration of each of its seasons. However, the seasonal behavior of a regional biota does not necessarily coincide with the seasons of the year as defined by calendar limits (Wolfe *et al.* 1949). Thus, climatic summaries based on monthly or calendar seasonal data are of little use in ecological studies. Since the phenological responses of a biota are correlated with certain sets of recurring climatic events rather than with arbitrary dates, attempts have been made to distinguish seasons on the basis of these regularly-occurring biotic events (Hopkins & Murray 1933, Wolfe *et al.* 1949).

Four biotic events are accepted as initiating the major seasons in deciduous forest communities. Spring begins with the first marked biological activity under and on top of the leaf litter; summer is initiated by canopy closure; fall commences with the first coloration of canopy foliage; and winter is marked by completion of leaf fall. Wolfe *et al.* (1949) point out that these major seasons often are marked by distinct subperiods of biological activity and propose the following 10 seasons: early, mid-, and late winter, early and late spring, early, mid-, and late summer, and early and late fall. This system was used in the present study.

As only one year's observations were available, the seasons on the Reserve during 1957 were delimited partly by phenological data and partly by seemingly

clear-cut meteorological events. The following remarks give some important seasonal characteristics and indicate how each season was defined.

Mid-winter began on December 25, 1956, when a light snow fell and initiated a snow cover which remained on the ground in most areas until early March, 1957. This was the coldest season of the year when both the annual low (-6.5°) and the lowest average temperature (17.0°) were recorded. Snowfall also was the heaviest of any season, totalling 12.4 in. The beginning of late winter was January 29 when there was a slight relaxation in a long cold spell. Winter ended with a period of warm weather prior to the beginning of spring.

Early spring began with a series of warm, sunny days lasting from March 12 to 16. Maxima rose to 69.5° on March 14 and minima did not fall below freezing during the period. Much biotic activity, particularly on south slopes, was observed. Virtually all biological activity was arrested by a period of low temperatures and intermittent snow from March 19 to April 10. The initiation of vigorous growth and flowering activity by the plants of the study area on April 15 marked the beginning of late spring. The first herbaceous flowers (*Hepatica americana*) were found on April 15 and by the second week of late spring numerous other species were flowering throughout the Big Woods. The first 3 weeks of late spring were warm and sunny. The latter part of late spring was characterized by several extended periods of cold, rainy weather. Nineteen species were observed to flower during late spring.

Early summer began on June 2 when the canopy of the Big Woods had closed. Considerable vegetative and reproductive activity took place during this season, particularly within the forest herbaceous layer. Almost 1/2 (30) of the species whose initial flowering date was observed were first observed during early summer. Although the annual maximum of 92.3° was recorded on June 18, average maxima were slightly below those of mid-summer. With the exception of one near-freezing night in early June, minima averaged in the mid-50's. Almost 1/4 of the total annual rainfall occurred during early summer. The beginning of mid-summer (July 14) was not marked by any striking biological event. However, as the season was characterized by extreme drought conditions the date of the last heavy rain in early July was taken as the end of early summer. Only 1 in. of rain fell during mid-summer and little of this wet the soil within the forests. Drought conditions became extreme late in mid-summer and diurnal wilting was observed in several herbaceous plants on south slopes. Mid-summer was the hottest season of the year, having the highest average temperature (69.4°) and average maxima (81.2°). Only 10 species were observed to flower during this season. Late summer began on August 24 when rains of moderate intensity broke the drought of mid-summer. Late summer was a transition period between summer and fall. No species were observed to flower in the woods,

although considerable flowering activity occurred in the fields.

Early fall began on September 17 when the first coloration was observed in the canopy and the first browning took place in the field layer. This season was one of drought, the most severe of the year, with only 0.6 in. of rain falling. The first frost of the year occurred on September 27. Coloration of tree leaves progressed rapidly after this and the height of fall color was during the first two weeks of October. Late fall was poorly-defined biologically, but seemed to begin on October 17 when a heavy rain broke the drought of early fall. Although all canopy foliage was dead during this season, the oaks retained many of their leaves. Little biological activity (except the flowering of *Hamamelis virginiana*) was noted.

Early winter began on November 9 when the first snow of the year fell. The 5 days following the snowfall had, in addition to low maxima, minima well below freezing. Snow fall during early winter totalled 7.5 in. and the average temperature was only slightly above freezing. Early winter ended on December 28 when a light snow fell. This snow was followed by others and many sites on the Reserve remained covered through late February, 1958.

METHODS

North- and south-facing slopes were chosen as sites for this study because of the great environmental and vegetational differences shown for such slopes in other studies (Potzger 1939, Shanks & Norris 1950, Cantlon 1953). Microenvironmental and vegetational sampling was carried out from March 17 to November 3, 1957. Data were obtained from 17 slopes, 9 north-facing and 8 south-facing. Slopes ranged from 31-60% in angle and deviated not more than 20° from true north or true south. Vegetation was sampled on 16 of these slopes, but microenvironmental data were recorded for only 4 north and 4 south slopes. Topographic features and canopy dominants for all plots are summarized in Table 2.

Although efforts were made to minimize all variables with the exception of topographic orientation, they were not entirely successful. In addition to orientation, an important variable was the presence or absence of protection as afforded by a facing slope. Thus, 4 groups of slopes were available: protected north slopes, open north slopes, protected south slopes, and open south slopes. The following data summarize the specific topographic characteristics of the sample sites:

Protected north slopes (Stations 1, 5, 6, 10, 16).

Station 1 was on the side of an esker facing into a kettle whereas Stations 5, 6, 10, and 16 were on the sides of kettles. Contours at all stations were concave.

Open north slopes (Stations 8, 11, 13, 15). Station 8 was on the side of a large kettle but, as the opposite side was over 500 ft distant, the

TABLE 2. Description of topographic and vegetational features of sample plots, E. S. George Reserve. (From Cooper 1960a).

Station	Slope %	Topographic position	Compass bearing	Leading canopy dominants
North slopes				
1*	53	Side of esker	N 16° W	<i>Quercus alba</i> , <i>Q. velutina</i> , <i>Prunus serotina</i> .
5†	42	Side of kettle	N 10° W	†
6†	36	Side of kettle	N 2° E	<i>Quercus alba</i> , <i>Prunus serotina</i> , <i>Acer rubrum</i> , <i>Q. rubra</i> .
8†	60	Side of kettle	N 18° E	<i>Quercus rubra</i> , <i>Q. alba</i> , <i>Acer rubrum</i> .
10	54	Side of kettle	N 10° E	<i>Quercus alba</i> , <i>Q. rubra</i> , <i>Acer rubrum</i> .
11	50	Side of outwash fan	N 4° E	<i>Carya ovalis</i> , <i>Quercus alba</i> , <i>Q. velutina</i> .
13	40	Side of esker	N 10° W	<i>Carya ovalis</i> , <i>Quercus velutina</i> , <i>Q. alba</i> .
15	51	Side of outwash fan	N 2° E	<i>Quercus rubra</i> , <i>Q. velutina</i> , <i>Carya ovalis</i> .
16	52	Side of kettle	N 18° W	<i>Carya ovalis</i> , <i>Acer rubrum</i> , <i>Quercus alba</i> .
South slopes				
2*	43	Side of esker	S 16° E	<i>Quercus velutina</i> , <i>Q. alba</i> , <i>Carya ovalis</i> .
3†	39	Side of esker	S 15° W	<i>Quercus velutina</i> , <i>Q. alba</i> , <i>Carya ovalis</i> .
4†	46	Side of esker	S 4° W	<i>Quercus velutina</i> , <i>Carya ovalis</i> , <i>Q. alba</i> .
7†	39	Side of kettle	S 7° W	<i>Quercus velutina</i> , <i>Prunus serotina</i> , <i>Q. alba</i> .
9	51	Side of esker	S 19° W	<i>Quercus velutina</i> , <i>Carya ovalis</i> , <i>Q. alba</i> .
12	50	Side of esker	S 14° E	<i>Quercus alba</i> , <i>Q. velutina</i> , <i>Q. rubra</i> .
14	41	Side of kettle	S 15° W	<i>Quercus velutina</i> , <i>Q. alba</i> , <i>Prunus serotina</i> .
17	31	Side of esker	S 20° W	<i>Quercus velutina</i> , <i>Carya ovalis</i> , <i>Q. alba</i> .

* Main station.

† Scattered stations.

‡ Not sampled.

facing slope offered no protection. Stations 11 and 15 were on the edge of an outwash fan and Station 13 was on the side of an esker. Contours at Stations 8 and 11 were concave and those at Station 13 were straight. Contours at Station 15 were slightly convex.

Protected south slopes (Stations 7, 14). Both of these stations were on the sides of kettles with concave contours.

Open south slopes (Stations 2, 3, 4, 9, 12, 17). These stations were all on the sides of eskers. Stations 2 and 12 actually faced into a large kettle but, as the opposite slope was approximately 500 ft distant, there was no real protection. Contours at Stations 2, 3, and 12 were essentially straight. At Stations 4 and 9 contours were slightly convex whereas at Station 17 contours were somewhat concave.

Although no historical data were available for the sample sites, it appeared that there had been no selective effects of grazing or lumbering on any slope or group of slopes. Thus, it was assumed that the

microclimatic and vegetational differences recorded were the results of real habitat differences rather than the past cultural practices of man.

MICROCLIMATES

Microclimatic data were derived from two independent series of instruments. One series, the "scattered stations," consisted of 3 north and 3 south slopes located at various points in the Big Woods, and the other, the "main station," of instruments disposed at the top, middle, and bottom of the north- and south-facing sides of an east-west trending hog-back (Table 2). Wooden thermometer holders in the middle of the slopes marked the locations of the scattered stations. Readings were taken at the scattered stations between 3:00 and 4:00 P.M. All readings, except soil moisture, were taken daily from March 31 to July 20, every other day from July 21 to September 14, and once weekly from September 15 to November 3. Soil moisture determinations were made once weekly from March 31 to November 3. Standard Weather Bureau instrument shelters, located 10 m apart on the horizontal, marked sampling locations at the main station. Readings here, except evaporation, were taken between 2:00 and 3:00 P.M. daily from March 17 to September 14 and once a week from September 15 to November 9. Evaporation data were gathered once a week from May 5 to October 24.

Light intensities at both the scattered and main stations and outside the Big Woods were recorded with a General Electric photocell having a range from 1-10,000 fc. Each reading was taken in the same place at each station. The meter was held 50 cm above the soil surface at an angle of 45° and oriented toward the south. Although field readings were recorded in foot candles, results were expressed as percentage of full light intensity recorded outside the Big Woods.

Maximum, minimum, and current air temperatures at the scattered stations were recorded with Six type maximum-minimum thermometers mounted under rotatable boards 10 and 50 cm above the soil. At the main station Casella hygrothermographs (Model 1040) were placed in the shelters at the top and bottom of each slope and thermographs (one Casella Model 760 and one Bendix-Friez Model 505) in the shelters at the middle of the slopes. The shelters were located so that the instrument recording elements were 50 cm above the soil. Only the maximum, minimum, and current temperatures obtained from the daily record were used in data analysis. In addition to the recording instruments, maximum-minimum thermometers were placed in the shelter and under boards 10 cm above the soil. Maximum, minimum, and current readings were taken from these.

Evaporation data were gathered at the main station only. Paired black and white Livingston porous-bulb atmometers were placed about 4 ft west of the instrument shelters. The bulbs were installed 50 cm above the soil on the usual field apparatus (Living-

ston 1935) with mercury and glass-wool valves to prevent backflow. Readings of total weekly evaporation in cc were taken by filling the reservoir bottle to a zero line. The field readings were multiplied by the supplied correction factor to give corrected values.

Current soil temperatures at the scattered stations were taken with a Weston probe thermometer (Model 2261) and at the main station with thermistors (Western Electric, Model 7A) embedded in fiberglass. The thermistor resistances were recorded with a Coleman Model 300 ohm meter. Correction coefficients were determined by means of a series of temperatures recorded at the installation sites with the probe thermometer. Readings at both sets of stations were taken at 2 cm and 20 cm below the soil surface. These depths approximated the A₁ and A₂ horizons.

Soil moisture values in the A₁ horizon at the scattered stations were determined by the gravimetric method. Composite samples, collected once a week, were oven dried, and soil moisture was expressed as percentage of oven-dry weight. Current soil moisture values at the main station were determined with fiberglass soil moisture units (Model 351) 2 cm and 20 cm below the soil surface. Resistance values were recorded with the Coleman meter. The fiberglass units were calibrated using field calibration of the area type (Reinhart 1953). Values were also expressed as percentage of oven-dry weight.

For most microclimatic factors, weekly averages seemed to express the trends of the data adequately. Thus, these values were used extensively in the analysis of data. As used in this study, average daily temperature is the sum of the daily maximum and daily minimum divided by two. Average weekly temperature is the sum of the weekly maxima and weekly minima divided by the number of readings. Average seasonal temperature is the sum of the seasonal maxima and minima divided by the number of readings. Temperatures, unless otherwise specified, are in °F.

VEGETATION

Vegetational sampling was carried out during July and August of 1957. On each of the 16 slopes sampled (Table 2) a plot 900 m², consisting of three tiers of three 100 m² plots, was laid out. Presence of all vascular plant species occurring in each subplot was recorded. Coverage of species in the field layer (within 4.5 feet of the ground) was determined by the line-intercept method. As plots were laid out on the horizontal, plant cover was recorded on the horizontal by means of two meter sticks arranged so that one was placed perpendicular to the horizontal and the other moved up or down along it until it was horizontal. The central 10 m of both diagonals of each of the subplots were measured with this device. Thus, 180 m of line-intercept data were available for each slope sample plot. The diameter at breast height of all trees over 1 in. d.b.h. and density of all shrubs and transgressives below 1 in. d.b.h. and over 4.5 ft high were determined in each subplot. In

addition, the total canopy cover of species over 1 in. d.b.h. was determined by pacing the four 30 m across-slope boundaries of the 3 tiers of subplots. The life-form of all species encountered was determined from winter and summer field observation during a part of 1956 and all of 1957 and by consulting other life-form studies of similar areas (Ennis 1928, McDonald 1937). Voucher specimens of all species are deposited either in the Reserve herbarium or in the author's collection. Nomenclature is that of Fernald (1950). Representative leaves were chosen from the voucher specimens and their areas determined both by tracings on millimeter graph paper and by the 2/3 length times width rule of Cain *et al.* (1956). The entire species list, showing both life-forms and leaf-size, may be found in Cooper (1958).

RESULTS: MICROCLIMATES¹

Because of the diversity of microenvironmental data recorded during the study, variations in each factor will be discussed independently. An attempt also will be made to summarize the cumulative effects of the various factors.

LIGHT

With respect to the light factor, three variables, intensity, quality, and duration are of ecological importance. Of these, only light intensity was assessed in this study.

From the pattern of variation in relative light intensity at the scattered stations (Fig. 1) several generalizations can be made concerning light conditions on the slopes. During the leafless season average relative light intensities exceeded 35% on south slopes and 25% on north slopes. However, the variation in the raw data was great, ranging from 8-100% on south slopes and from 6-95% on north slopes. As the canopy closed with the beginning of late spring, light intensities dropped rapidly. This decline continued until the first week in June when the forest canopy had completed development. At all times during the drop in light intensity, and during all of summer, light intensities on south slopes exceeded those on north slopes. With leaf abscission in the fall, light intensities on both slopes increased rapidly to the leafless season peaks.

In general, the shapes of the curves were the same on both slopes. This seemed to indicate that variations due to cloudy days, which would tend to raise relative light values, were similar on both slopes. However, the period of canopy closure in early late spring was an important exception. The curve of relative light intensity on north slopes diminished continuously from the week of April 21 until the beginning of summer. On south slopes, on the other hand, the continuous decline did not begin until the week of April 28 and the greatest difference in relative light intensity (16%) between the slopes occurred during this week. Thus, the effects of canopy closure were

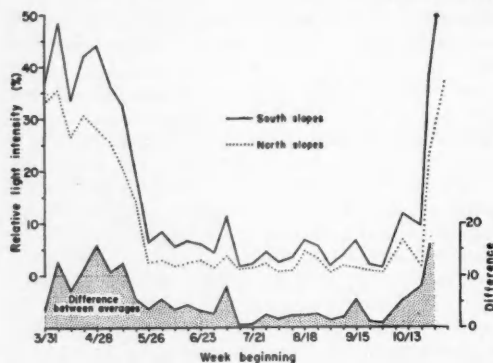


FIG. 1. Weekly average mid-afternoon relative light intensity (% of light in the open) at scattered stations. Each value is an average of the weekly averages at the 3 north or 3 south slopes.

first felt on north slopes and relative light values declined most rapidly on those slopes.

Data from the main station (Table 3) generally were similar to those from the scattered stations, but they show in addition the variations in light intensity occurring from top to bottom of the slopes. The seasonal averages show that, with the exception of early fall, light intensity was always greatest at the top of the south slope and diminished downslope. The pattern on the north slope was not as clear. In spring, early summer, and late summer, relative light values decreased from slope top to bottom. However, in mid-summer and fall, values were highest in the middle of the north slope. These changes may be due to the variable effects of dense canopy in relation to the position of the sun. Despite these variations, the bottom of the north slope always had the lowest intensities recorded.

TABLE 3. Seasonal average relative light intensity (percentage of light in the open) at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring.....	55.3	52.2	52.3	35.7	33.5	32.5
Late spring.....	43.7	43.4	38.4	25.6	23.8	20.3
Early summer.....	8.0	7.6	5.5	1.8	1.7	1.3
Mid-summer.....	6.1	5.1	4.0	0.7	1.0	0.7
Late summer.....	9.2	6.3	6.0	1.4	1.3	1.1
Early fall.....	12.3	10.0	13.0	3.2	3.4	2.7
Late fall.....	57.3	56.2	44.9	13.8	15.5	13.9
Average.....	27.4	25.8	23.4	11.7	11.5	10.4

Analysis of light intensities during the period of canopy closure at the main station showed variations in the amounts of high-intensity light at various positions on the slopes. These differences were due to the differential effects of canopy closure on the slopes. At the bottom of the north slope, light intensity first passed under 10% on May 9 and it remained per-

¹ All original microclimatic data are included in Vol. 2 of Cooper (1958).

manently under this level after May 20. At the top and middle of the north slope intensities did not pass under the 10% level for the remainder of the growing season until May 24. On the south slope the first day under 10% at the top and bottom of the slope was May 26 and, in the middle of the slope, May 28. All stations passed more or less permanently below 10% on June 6. Thus, there was a longer period of low light intensity during the growing season on the north slope as there was a period of almost one month during which intensities fell below 10% on the north slope while remaining well above this level on the south slope. During summer no values over 10% of full light occurred on the north slope. However, on the south slope such readings were recorded between 8 and 13 times. The maximum relative light intensity recorded during summer on the south slope ranged from 22.7-36.3% whereas on the north slope it never exceeded 6.7%.

AIR TEMPERATURE

Variations in air temperature within forests and on north and south slopes have been investigated more intensively than variations in any other microclimatic factor. The present study also gave the greatest share of attention to temperature phenomena.

AVERAGE TEMPERATURE

Average air temperature data were useful to summarize gross differences between the slopes and to approximate general temperature patterns during the period of the study.

South slopes had higher average air temperatures throughout the entire growing season as data from the 50 cm level at the scattered stations show (Fig. 2). The differences between the slopes were least in the first two weeks of late spring before the canopy had closed. In this period more radiation penetrated to the surface on the north slope than during any other season. With canopy closure, air temperatures on the south slopes were consistently higher than those on north slopes. The greatest difference was during mid-summer when averages were 7-8° higher on the south slopes. During late summer and fall tem-

peratures were almost uniformly 2-4° higher on south slopes. The two major dips in the curves, one in mid-May and the other in late June and early July, were due to periods of cool, rainy weather which affected both slopes uniformly.

Average seasonal temperature data from the 10 cm and 50 cm levels at the main station (Table 4) show that temperatures at both levels on the south slope generally exceeded those on the north slope during the entire growing season. During spring, temperatures were higher close to the ground on both slopes but the gradient was always steepest on the south slope, averaging 4-5° in early spring and 3-4° in late spring. During summer, temperatures continued warmest near the ground on the south slope and at the top of the north slope. Gradients were generally less than in spring except at the top of the south slope where the increase was 5°. Temperatures at the middle and bottom of the north slope were, with one exception, slightly higher at 50 cm than at 10 cm. Thus, temperature conditions characteristic of a mature forest were found only during summer and only at the lower stations on the north slope. The data further show that, in general, the highest average temperatures occurred at the top of the south slope and that temperatures diminished slightly down-slope whereas the lowest averages consistently were recorded at either the middle or bottom of the north slope.

TABLE 4. Seasonal average temperatures at 10 cm and 50 cm levels at main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
10 cm	40.3	40.1	*	°	36.2	36.5
50 cm	36.1	36.0	35.7	35.3	35.2	34.6
Late spring						
10 cm	62.7	62.5	62.1	60.0	58.7	59.1
50 cm	59.1	59.1	58.9	58.4	58.4	58.0
Early summer						
10 cm	69.9	70.4	69.9	68.1	66.4	66.9
50 cm	67.9	67.8	67.6	67.3	67.6	67.2
Mid-summer						
10 cm	75.0	72.9	71.8	69.9	68.9	69.4
50 cm	69.9	69.7	69.5	68.2	69.4	68.8
Late summer						
10 cm	67.1	66.1	66.7	64.3	63.1	63.0
50 cm	64.4	64.5	64.2	63.6	63.9	63.5
Early fall						
10 cm	58.0	58.0	59.2	55.8	54.6	54.8
50 cm	54.0	54.1	53.7	53.4	53.2	52.6

* Insufficient data.

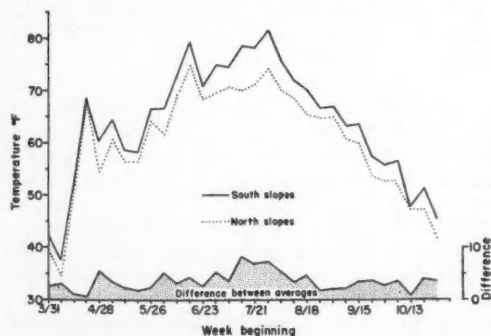


FIG. 2. Weekly average air temperature at the 50 cm level at scattered stations. Averages computed as in Fig. 1.

MAXIMUM TEMPERATURES

Although average temperatures were useful for illustrating general patterns, extremes of temperature (maxima and minima) showed greater variation and thus more clearly illustrated the differences between the air temperature regimes of the slopes.

The greatest and most consistent differences in air temperature between the slopes were in the maximum temperature area. Average weekly maxima and

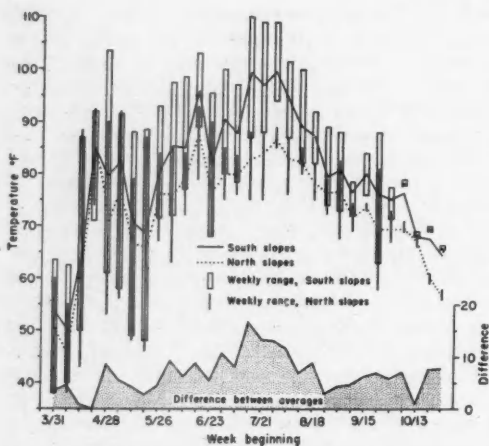


Fig. 3. Weekly average maximum air temperature and weekly range in maximum air temperature at 50 cm level at scattered stations. Averages computed as in Fig. 1.

ranges in maxima at the 50 cm level at the scattered stations (Fig. 3) showed that very different maximum temperature regimes characterized the slopes during the period of the study.

On north slopes maxima rose rapidly early in late spring and averaged in the 80's during the week of April 21. Maxima declined through the remainder of late spring, first under the influence of canopy development and then in response to the period of cool, cloudy weather in May. The greatest ranges in maxima on north slopes occurred during early late-spring. During summer two peaks of maxima occurred, one in June and the other in July. However, neither of these exceeded 90° and average maxima generally ranged between 75° and 85°. Ranges of maxima exceeded 90° only during the week of June 16.

On south slopes, however, average maxima were much higher throughout most of the growing season. During early late spring averages and ranges were very similar to those on north slopes. In the final weeks of late spring maxima declined but still averaged 3-5° higher than on north slopes. During summer, maxima were considerably higher than on north slopes with averages over 90° for half of the 12 weeks of early and mid-summer. Maxima exceeded 90° during every week of summer.

Thus, on north slopes maxima showed the most variation in spring before canopy closure and during the remainder of the growing season relatively stable conditions prevailed. On south slopes, however, there was the same period of high spring maxima, but this was followed by a period of even higher maxima during summer. These regimes were comparable to those of thinly-forested and cove stations at Neotoma Valley (Wolfe *et al.* 1949). The south slope regimes agreed with those of thinly forested stations where temperatures rose sharply to

a spring maximum, leveled off, and then returned to or exceeded the spring maximum in late summer or early fall. North slope regimes, however, resembled those of deep coves where temperatures rose rapidly in early spring and then leveled off for the remainder of the growing season.

The least differences between the maximum temperature regimes of the slopes occurred during the first 2 weeks of late spring before canopy closure had taken place. Both slopes had average maxima of 85° during the week of April 21 and ranges on the north slope actually were greater than those on south slopes during this period. As all north slopes were located on the sides of kettles, this phenomenon may be related to temporary retention of heated air within the kettles. However, the effects of canopy closure were immediately manifested on the north slopes by a great reduction in the extremes of maximum temperature. The highest average maxima on north slopes occurred during the week of the summer solstice (June 16) when the sun was at its highest in the sky and was falling most directly on the north slopes. Differences between the slopes were greatest in mid-summer when the sun shone almost directly on the south slopes, but the combination of canopy and lowered angle of incidence produced less incoming radiation on the north slopes.

Maximum temperature conditions at the main station (Table 5) were similar to those at the scattered stations. However, because of the ameliorating effects of the instrument shelters, extremes at the 50 cm level were not as high as those recorded on the thermometers at comparable levels at the scattered stations. Wolfe *et al.* (1949) found a similar situation with respect to minimum temperatures and showed that minima recorded within a standard shelter were consistently higher than those to which plant parts appeared to be exposed. The data of this study support a similar conclusion with respect to maximum temperatures. Despite these inadequacies, certain patterns in maximum temperature regimes can be drawn from the main station data. These patterns illustrate general maximum temperature regimes, and more important, maximum temperature gradients in the air layer near the ground during periods of occurrence of the "incoming radiation type" (Geiger, 1957).

During early spring, maxima were higher at all stations on the south slope, and the gradient between maxima at 50 cm and those at 10 cm was much greater on south slopes. This gradient amounted to 10° at the top of the south slope and was only half as great at the bottom of the north slope. With the transition to late spring, maxima rose abruptly on both slopes. Temperatures continued to increase toward the ground on both slopes, but the steepest gradients still were on the south slope. On the north slope the annual maximum of 96° occurred during the week of April 28. During this period of maximum solar radiation on the north slope, air at the bottom of the slope in the kettle became intensely heated, and thus un-

TABLE 5. Seasonal average maximum temperatures at 10 cm and 50 cm levels at main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
10 cm.....	55.5	54.1	*	*	47.7	49.0
50 cm.....	45.5	45.5	45.0	44.3	43.9	44.0
Late spring						
10 cm.....	78.0	77.8	77.6	73.0	71.7	73.3
50 cm.....	70.7	70.6	70.8	70.0	69.4	70.1
Early summer						
10 cm.....	81.2	82.3	81.5	77.7	75.4	76.4
50 cm.....	78.0	77.5	77.5	76.9	76.8	76.4
Mid-summer						
10 cm.....	90.0	86.0	84.3	80.1	79.0	79.9
50 cm.....	81.2	80.5	80.8	79.2	79.4	78.6
Late summer						
10 cm.....	77.8	75.9	77.4	72.3	71.1	70.7
50 cm.....	73.8	73.7	73.5	72.1	71.9	71.4
Early fall						
10 cm.....	73.6	74.4	77.2	69.9	68.5	68.3
50 cm.....	65.0	65.0	64.8	64.1	63.0	62.4

* Insufficient data.

stable. Small parcels of air were seen to escape up the sides of the kettle as miniature "dust-devils" with leaves in their vortices. These also occurred on the south slope under the intense heating of early late spring. They were observed at no other time during the study at any location. On the north slope, increasing temperatures toward the ground were characteristic of the first 3 weeks of late spring. However, after canopy closure, temperatures in the air layer near the ground approached those of densely-forested areas and by the week of May 26 both the bottom and middle of the north slope had lower weekly maxima at 10 cm than at 50 cm.

During summer, maxima at 50 cm were confined to a relatively narrow range on both slopes. This condition was in contrast to the pattern at the scattered stations where maxima on south slopes rose to an annual high during mid-summer and may be explained by the modifying effect of the shelters on maximum temperature readings. The mid-summer peak was apparent at 10 cm and was particularly marked at the top of the south slope where an annual maximum of 102° was reached during the week of August 18. Maxima averaged higher near the ground at all south slope stations and at the top of the north slope throughout all of summer. At the bottom and middle of the north slope average maxima were, with one exception, greater at 50 cm than at 10 cm. Thus, during summer, maximum temperature stratification at the lower stations on the north slope was that of well-developed forests whereas on the south slope and at the top of the north slope a weak version of the incoming radiation type typically developed.

During early fall, maxima were similar to those of late summer with temperatures at 50 cm slightly higher on the south slope and those at 10 cm considerably greater. Maxima increased from 50 cm to 10 cm at all stations, but again gradients were greater

on the south slope. The opening of the canopy during late fall allowed considerable heating of the south slope, but because of the lowering of the sun in the sky, this factor had little effect on the north slope. Thus, maxima were much higher on the south slope during this season, particularly at 10 cm.

MINIMUM TEMPERATURES

Minimum temperature regimes did not show the great variations characteristic of maximum temperature regimes. Limited observations at the main station indicated that the lowest minima generally occurred at the bottoms of the slopes and the highest at the tops. The lowest minimum recorded at any station was -5° at the bottom of the north slope during the weeks of January 4 and 11, 1958.

Average weekly minima and minimum temperature ranges at the scattered stations (Fig. 4) illustrate general conditions on the slopes. During spring, minima were consistently lower on the north slopes. The differences were greatest in early spring and became progressively less toward summer. No great differences in minima were found in summer and during 5 weeks, minima actually averaged higher on north slopes. The greatest ranges in minima on both slopes occurred during the first week of late spring. The first day of late spring (April 16) was preceded by 4 nights of sub-freezing temperature. April 14 and 15 were clear with maxima well into the 50's. On the night of April 15 the temperature failed to fall below freezing at any of the stations and sub-freezing temperatures were not recorded anywhere in the study area until 17 days later on the night of May 2. The accelerated period of plant activity marking the beginning of late spring seemed a response to this abrupt change in minimum temperature regime. The only other ranges of minimum temperature in excess of 25° occurred in early spring. During the remainder of the growing season no wide ranges in minima were recorded and there were no significant differences between ranges on north and south slopes.

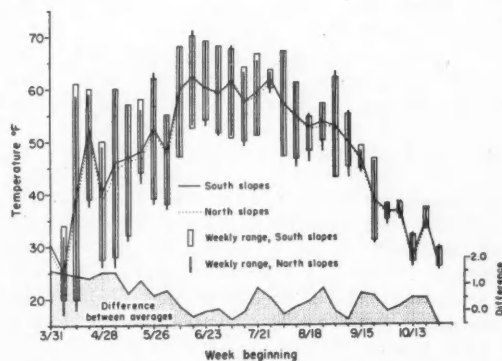


FIG. 4. Weekly average minimum air temperature and weekly range in minimum air temperature at 50 cm level at scattered stations. Averages computed as in Fig. 1.

Despite the small differences in minimum temperature regimes at the main station certain patterns were found. Here also minima showed most variation during the early growing season. During early spring and the first weeks of late spring there was a consistent tendency for the highest minima to be recorded at the top or middle of the south slope and for minima to diminish down slope. On the north slope during this period a similar progression was observed and the lowest minima at all stations almost always were recorded at the bottom of this slope. However, during the last three weeks of late spring, presumably under the influence of the developing canopy, variations in minima became negligible. Minimum temperature variations in summer were slight. In fact, the diurnal low often was recorded at stations on the south slope, a circumstance probably associated with the thinner south slope canopy which permitted the escape of greater amounts of outgoing radiation at night than did the thicker canopy of the north slope. In fall, patterns were similar to those of summer, with little marked difference between the slopes. During late fall there was a trend toward lower minima on the north slope indicating a transition to winter conditions.

The consistent presence of the lowest weekly minima at the bottom of the north slope during the first 3 weeks of late spring may be explained in terms of cold air drainage patterns. In the evening the soil and low vegetation on the sides of the kettle above this station radiated heat and temperatures dropped within the lower layers of air. This cooled air flowed down the sides of the kettle replacing warm air which occupied the kettle during the day. As cold air accumulated in the kettle a "cold air lake" was formed. When the level of this lake passed the level of the instruments at the bottom of the north slope, a marked drop in temperature was registered. Thermograph charts during this period often recorded this phenomenon, and abrupt drops in temperature of 4-8° between 7:40 and 8:35 P.M. were not uncommon. The abrupt drop was always preceded by a slight rise in temperature associated with the forcing upward by the cold air of warm air which had filled the kettle during the late afternoon. The cessation of this pattern during the last part of late spring was due to a decrease in nocturnal outgoing radiation associated with canopy closure.

Minima were most often recorded during the hours of early dawn when the "outgoing radiation type" (Geiger, 1957) had developed. A condition often associated with nocturnal minima is the development of a temperature reversal, or inversion, near the ground.

Comparison of minima from the 10 cm and 50 cm levels at the main station indicated that pronounced inversions were recorded during early spring and the first weeks of late spring (Table 6). During the first 3.5 weeks of late spring inversions occurred at all stations. On the south slope and at the top of the north slope 10 cm minima averaged about one degree

TABLE 6. Comparison of occurrence and magnitude of inversions during late spring at main station.

Temperature difference between 10 and 50 cm	South top	South middle	South bottom	North top	North middle	North bottom
<i>April 16-May 9</i>						
0.1-1.0	1	1	0	0	0	0
0.0	3	3	5	8	0	1
-0.1-1.0	10	14	8	11	2	9
-1.1-2.0	8	6	10	5	9	9
-2.1-3.0	1	0	1	0	9	4
-3.1 plus	1	0	0	0	4	1
Mean	-1.2°	-1.0°	-1.2°	-0.8°	-2.4°	-1.6°
Nights with inversions (%)	83%	83%	78%	67%	100%	100%
<i>May 19-June 1</i>						
2.1-3.0	2	1	1	0	0	0
1.1-2.0	5	1	1	5	0	2
0.1-1.0	12	8	5	12	0	6
0.0	4	10	15	6	5	3
-0.1-1.0	0	3	1	0	13	9
-1.1-2.0	0	0	0	0	4	3
-2.1-3.0	0	0	0	0	1	0
Mean	1.1°	0.3°	0.3°	0.9°	-1.0°	-0.3°
Nights with inversions (%)	0%	13%	4%	0%	78%	52%

below those at 50 cm whereas at the middle and bottom of the north slope 10 cm minima were 2.4° and 1.6° respectively below those at 50 cm. Thus, early in late spring, before the canopy and low plant cover had fully developed, inversions occurred on both slopes.

On May 10 an abrupt change occurred in the pattern and distribution of inversions. From this date through the close of late spring and throughout the remainder of the growing season inversions rarely were recorded on the south slope and at the top of the north slope. In fact, minima were generally higher at 10 cm than at 50 cm. At the lower stations on the north slope inversions continued to form but they were lower in magnitude than during the first part of late spring. An explanation for this shift in appearance of inversions may lie in the development of the ground layer vegetation on the slopes. A low plant cover spreads out the region of daytime heat absorption and the region of heat loss at night (Geiger, 1957), and a dense cover can hold cold air above it by the interference of its vegetative parts. Thus, on the south slope where the ground layer was better developed the low vegetation acted as a buffer zone for night-time extremes in temperature and prevented inversions from forming. On the north slope, however, the sparser ground layer was ineffective in this role and a weak inversion typically developed. During summer, the lowest average minima at 50 cm at the main station actually occurred on the south slope. At this level there was no protection from the

low plant cover and, because of the thinner canopy on this slope, heat exchange with the air outside the forest took place more freely than on the north slope. Thus, on the average, minima at 50 cm on the north slope were higher than those at comparable levels on the south slope.

WIND

No detailed data on wind variations in the study area were collected. However, several limited observations illustrated variations in the climate of the slopes at the main station related to differences in wind direction and velocity.

A brief study of wind variability at the main station was carried out on May 4, 1957.² Measurements of maximum, minimum, and average velocities and of wind direction at mid-day were taken at 4 stations on both slopes. Due to the direction of the wind, from the north-northwest, wind speeds were higher at each station on the north slope than at corresponding stations on the south slope. Velocities were highest at the slope tops and decreased down slope. The lowest velocities were recorded at the bottom of the south slope. The data also showed that wind speeds were considerably lower at 10 inches above the ground than at 5 ft, particularly at the slope bottoms.

There was evidence that such modified wind patterns appeared to exert some effect on daytime temperature regimes on the slopes (Table 7). On calm summer days, for example, the incoming radiation type was well-developed at all stations, particularly on the south slope. Intense solar radiation heated the air layer near the ground and, as there was little air movement to cool these sites, temperatures near the ground were extremely high. However, on days when there was a recognizable wind from the south or southwest, the incoming radiation type was not as strongly developed. The bottom and middle stations on the south slope appeared to be least affected by the wind, whereas the two stations most affected were those at the tops of the slopes.

TABLE 7. Average mid-afternoon air temperature at 10 cm and 50 cm levels on clear, calm days and clear, windy days during summer at the main station.

Station	AIR CALM ^a		WIND FROM SOUTH OR SOUTHWEST ^b	
	10 cm	50 cm	10 cm	50 cm
South top.....	84.5	81.1	79.4	78.9
South middle.....	83.6	80.3	79.9	78.5
South bottom.....	83.4	80.6	80.9	78.9
North top.....	80.2	79.2	78.3	78.3
North middle.....	78.9	79.4	76.6	78.4
North bottom.....	79.1	78.4	77.1	77.6

^a Average of 7 days.

^b Average of 4 days.

² The author is indebted to E. W. Bierly and J. S. Marshall for collecting these data and to Dr. A. N. Dingle for permission to use them.

EVAPORATION

Evaporative water loss from soil and plant surfaces is an important microclimatic factor. Despite the fact that evaporation is dependent on other physical phenomena (radiation, air movement, etc.) it is a useful measure of the environmental differences between various sites. The instrument measuring water loss integrates evaporation-influencing factors and, in this respect, behaves as a plant by responding to the sum of factors rather than to each individually.

The fact that evaporation was greatest on the south slope throughout the study was shown by cumulative data from black and white bulb atmometers (Table 8). In fact, evaporation from white bulbs on the south slope exceeded that from black bulbs on the north slope. Evaporation for the season took place in a straight-line fashion, each 4-week increment approximately equalling that of the previous period. There was no evidence of a reversal to winter conditions with diminished evaporation because measurements were concluded before the cool, rainy weather of late fall and winter began.

TABLE 8. Total evaporation and evaporation factors at main station, May 5-October 24, 1957.

Station	Total evaporation (cc)	Factor
<i>North slope</i>		
Bottom: White bulb.....	1457	1.00
Black bulb.....	1601	1.00
Middle: White bulb.....	1629	1.12
Black bulb.....	1800	1.12
Top: White bulb.....	1803	1.24
Black bulb.....	1965	1.23
<i>South slope</i>		
Bottom: White bulb.....	2044	1.41
Black bulb.....	2430	1.52
Middle: White bulb.....	2168	1.49
Black bulb.....	2694	1.68
Top: White bulb.....	2225	1.53
Black bulb.....	2722	1.70

The general pattern of water loss through the growing season was similar for each of the locations sampled. During late spring evaporation dropped sharply due to canopy closure and attendant lowering of solar radiation and air movement within the trunk-space area. Several periods of accelerated evaporation occurred. These were related to periods of clear, warm weather. The most marked of these was during mid-summer when little rain fell and weeks were characterized by a high percentage of cloudless, sunny days. From this mid-summer peak, evaporation fell off through the remainder of the summer and increased during the dry fall when trees began

to lose their leaves. Although water loss patterns were similar at all locations, total loss was considerably higher on the south slope and there was a pattern of highest evaporation at the top of each slope and least at the bottom.

Using the atmometer pair at the bottom of the north slope as a standard, evaporation factors were established for the various locations (Table 8). These data show the differences both between slopes and with position on the slopes. Total black and white bulb evaporation both increased by approximately 12.5% increments up the north slope. The similarity between the percentage increases was probably due to the low levels of light intensity occurring throughout most of the growing season on the north slope. On the south slope, however, white bulb evaporation was much greater than on the north slope, varying from 1.4 to 1.5 times as great from slope bottom to top. Black bulb evaporation was also much greater and showed a similar increase from bottom to top of slope. However, black-bulb values were higher than their white-bulb counterparts, a fact probably explained by the greater solar radiation received on the south slope.

SOIL TEMPERATURE

Because of the equipment used, soil temperatures recorded in this study were obtained at only one time during the diurnal period. Such data have certain limitations. Muttrich (1880, in Li 1926) showed that these data were not a safe basis for the calculation of mean soil temperatures and that they could be used only on a comparative basis (as in the present study). Thus, maximum and minimum daily temperatures would be more desirable for describing annual and diurnal temperature regimes.

Furthermore, the comparative value of the mid-afternoon readings obtained in this study is complicated by the different diurnal temperature regimes which characterized the slopes. A short study of diurnal soil temperature patterns at the main station on May 4, 1957, showed that maxima in the A_1 horizon were attained earlier on the south slope (1:00 to 2:15 P.M.) and later (2:30 to 3:45 P.M.) on the north slope. In the A_2 horizon, temperatures rose continually during the afternoon and maxima at this depth on both slopes were not reached until late in the afternoon. Thus, by sampling soil temperature between 2:00 and 4:00 P.M., temperatures slightly below diurnal maxima were recorded in the A_2 horizon on both slopes and in the A_1 horizon on south slopes. Only A_1 horizon readings on north slopes approximated maxima for the day at those locations. Despite these limitations, the data obtained were useful in contrasting soil temperature regimes on the slopes.

The general trend of soil temperatures in the A_1 and A_2 horizons was shown by average weekly temperatures from the scattered stations (Fig. 5). South slopes were characterized by warmer soil temperature regimes than north slopes. In early spring temperatures in the A_1 horizon exceeded 50° on south

slopes while remaining at or below freezing on north slopes. Soil temperatures rose rapidly on both slopes during late spring. The greatest temperature range in the A_1 horizon on both slopes occurred during the first week of late spring. During the next 2 weeks, before the canopy had fully developed, maxima reached 73° on south slopes and 69° on north slopes. Increase in temperature in the A_2 horizon lagged behind that in the A_1 , the lag being greater on north slopes. The A_1 and A_2 horizons on south slopes and the A_1 horizon on north slopes all reached their spring maxima during the first 2 weeks of early spring whereas the A_2 horizon on north slopes did not reach its spring maximum until the last week of late spring.

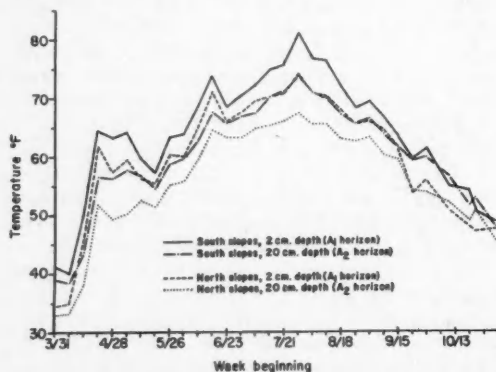


FIG. 5. Weekly average mid-afternoon soil temperature in A_1 and A_2 horizons at scattered stations (from Cooper 1960a). Averages computed as in Fig. 1.

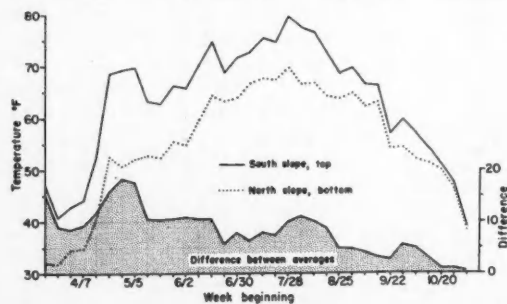
Annual maxima were reached in both horizons and on both slopes during mid-summer. Maxima were higher on south slopes and temperatures averaged 3-6° higher at similar depths on south slopes throughout most of summer. Differences in soil temperature diminished through late summer and early fall and were least in fall when there was an approach to the winter type of temperature profile with warmer temperatures deeper in the soil.

Seasonal average soil temperatures from the main station showed the variations due to slope position (Table 9). Seasonal soil temperatures in both the A_1 and A_2 horizons were always highest on the south slope. Furthermore, during practically every season values decreased progressively from a high at the top of the south slope to a low at the bottom of the north slope. Differences between the slopes were greatest during late spring when values were 10-12° higher on the south slope than at similar stations on the north slope. Other seasons of major difference were early spring and mid-summer when comparable values were 8-10° and 6-7° higher on the south slope. Differences between the slopes were least in fall when, due to the lag effect, temperatures on the north slope were dropping proportionately slower than those on the south slope.

TABLE 9. Seasonal average soil temperatures in the A₁ and A₂ horizons at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
A ₁	43.3	43.6	41.2	34.4	33.5	33.4
A ₂	38.5	38.6	37.6	33.4	32.6	33.1
Late spring						
A ₁	65.0	64.9	61.7	53.2	52.2	51.2
A ₂	55.5	55.5	53.6	48.9	48.3	47.4
Early summer						
A ₁	70.7	69.1	67.7	64.3	64.2	63.5
A ₂	64.9	64.2	63.2	60.6	60.1	59.2
Mid-summer						
A ₁	76.2	75.2	72.7	69.6	68.3	67.0
A ₂	70.1	68.7	67.2	65.8	65.3	64.5
Late summer						
A ₁	68.2	67.5	68.2	65.6	65.2	63.7
A ₂	65.6	64.8	64.1	62.8	62.4	62.1
Early fall						
A ₁	60.3	60.8	60.4	57.9	57.2	56.5
A ₂	58.5	58.3	57.2	56.4	56.0	56.0
Late fall						
A ₁	50.0	48.7	50.2	49.0	48.5	48.7
A ₂	50.8	50.7	49.5	49.3	48.7	50.0

That there were four periods of major differences in soil temperatures at the main station can be shown by weekly average A₁ horizon values from the top of the south slope and bottom of the north slope (Fig. 6). The first period of difference was in early spring when the soils of the south slope had thawed and warmed whereas the soil at the bottom of the north slope remained frozen. Although data for this season were incomplete, over one-half of all readings on the south slope were above 40° whereas no readings this high were recorded on the north slope (Table 10). Conversely, temperatures of freezing and below were recorded regularly at the middle and bottom of the north slope, and not at all on the south slope. The first 4 weeks of late spring marked the second, and greatest, period of difference in soil temperature. During this season, before canopy closure, temperatures in the soil rose rapidly on both slopes. However, temperatures on the south slope rose higher and fluctuated more than those on the north slope (Table 10). Almost half of the temperatures recorded on the south slope during this period were

FIG. 6. Weekly average mid-afternoon soil temperature in A₁ horizon at top of south slope and bottom of north slope at main station.TABLE 10. Distribution of mid-afternoon A₁ horizon soil temperatures at the main station in various temperature intervals during selected seasons.

Temperature interval	NUMBER OF DAYS					
	South top	South middle	South bottom	North top	North middle	North bottom
<i>Early spring</i>						
— 32.0.....	0	0	0	1	10	11
32.1 - 40.0.....	10	9	11	25	16	15
40.1 - 48.0.....	12	10	13	0	0	0
48.1 - +.....	4	7	2	0	0	0
<i>First four weeks of late spring</i>						
32.1 - 40.0.....	0	0	0	2	2	3
40.1 - 48.0.....	2	1	2	5	5	6
48.1 - 56.0.....	2	3	3	13	12	18
56.1 - 64.0.....	7	8	11	7	8	0
64.1 - 72.0.....	7	5	10	0	0	0
72.1 - 80.0.....	8	9	1	0	0	0
80.1 - +.....	1	1	0	0	0	0
<i>Mid-summer</i>						
60.1 - 68.0.....	0	0	1	19	17	24
68.1 - 76.0.....	21	24	34	21	23	16
76.1 - 84.0.....	19	16	5	0	0	0

over 64° whereas no temperatures of this magnitude were recorded on the north slope.

The other periods of difference occurred during periods of high air temperature and low rainfall in mid-summer and early fall. The differences during mid-summer were particularly striking (Table 10). At the upper stations on the south slope almost half of the temperatures recorded were over 76°, whereas less than one-quarter of the readings at the upper stations on the north slope were of this magnitude. Furthermore, the lowest temperature recorded at the top of the south slope during this period was 71° whereas the highest temperature recorded at the bottom of the north slope was 72°. Thus, there was practically no overlap between soil temperature ranges at these two stations. Examination of the temperature distributions (Table 10) showed that the stations topographically-intermediate between these two extremes had intermediate temperature distributions.

Although no quantitative measurements were made, observations during the winters of 1957 and 1958 indicated that different temperature conditions prevailed in the surface soils of the slopes during this season (Cooper 1960a). Winter snow covers were seldom of long duration on south slopes. Snow usually melted soon after falling and there was seldom any great accumulation. North slopes, on the other hand, had a more or less continuous snow cover throughout most of mid-winter. The surface soils on south slopes underwent numerous cycles of freezing and thawing, particularly on warm, sunny days, whereas the soil remained frozen continuously under the snow cover of north slopes. Even after snow had melted in early spring the soils of some north slopes remained frozen several weeks longer than soils on south slopes. By March 31, 1957, for example, no frost was found in any south slope soil, whereas frost was still

encountered as late as April 4 and April 17 on two north slopes.

SOIL MOISTURE

As would be expected, there were differences between the soil moisture regimes of the slopes. Average weekly values from the scattered stations showed that north slopes had higher amounts of moisture in the A₁ horizon throughout almost the entire growing season (Fig. 7). With the exception of one week, average values were always lower on south slopes. There was an abundance of soil moisture on both slopes during all of spring. There was a rapid decline in soil moisture during early summer but the heavy rains of the last two weeks of this season raised levels again. Mid-summer was a period of extreme soil-moisture depletion with little or no rain falling during this period of annual maximum temperatures. Even during this period of drought soil moistures were higher on north slopes. Heavy rains in late summer raised soil moisture levels slightly, but these reserves were rapidly depleted by a long period of drought (22 days) during early fall. With the beginning of late fall soil-moisture values began to return to the high levels of winter and early spring.

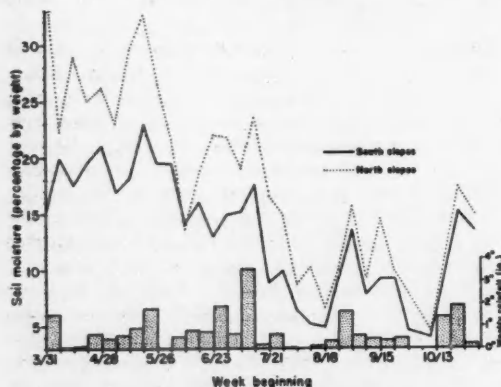


FIG. 7. Weekly mid-afternoon soil moisture (per cent by weight) in A₁ horizon at scattered stations (from Cooper 1960a). Averages computed as in Fig. 1.

The mid-summer drought when many plants, particularly those of south slope field layers, were still active vegetatively and reproductively, appeared to be of importance to plant distributions in the study area. During this lengthy dry period soil moistures probably dropped close to the permanent wilting point on both slopes. The drop was more marked on south slopes and this, coupled with the high air temperatures and evaporation rates of these sites, undoubtedly has been important in limiting the distribution of species with higher moisture requirements on south slopes. The mid-summer moisture stress of these sites was indicated by the fact that several species (*Amphicarpa bracteata*, *Lysimachia quadrifolia*, *Monarda fistulosa*, and *Phryma leptostachya*) under-

went brief mid-afternoon wilting several times during the week of August 11-17. These conditions were in marked contrast to those of north slopes. When soil-moisture conditions became critical during mid-summer on those sites, maximum temperatures were low enough so that the great evaporation stress of south slopes was not present. Wolfe *et al.* (1949) called attention to a similar situation with regard to maximum temperature variations between cliff and forest habitats at Neotoma. Furthermore, many late-aestival and autumnal flowering species of the south slopes carried on their entire reproductive cycle during the period of extreme moisture stress in late summer or fall whereas on north slopes more species were vegetatively and reproductively active during spring when there was abundant moisture in the soil.

Seasonal percentages at the main station (Table 11) supported the generalizations derived from the scattered station data. During early spring there was a large amount of moisture in the soil on both slopes. More moisture was present in the A₂ horizon during early spring than during any other part of the growing season. Soil moistures at all stations remained relatively high during late spring and early summer but during mid-summer values averaged lower than any other season except early fall. During these dry periods values at each station, with the possible exception of the bottom of the north slope, undoubtedly approached the permanent wilting point. At the bottom of the north slope during the drying cycles moisture values in the A₁ horizon were higher than at other stations. This was due to the lower soil temperatures, air temperatures, and evaporation rates at this site. Also, the heavy litter layer prevented a considerable amount of direct evaporative water loss from the soil.

The pattern of daily soil-moisture values in the A₁ horizon at the top of the south slope and the

TABLE 11. Seasonal average soil moisture (percentage by weight) in A₁ and A₂ horizons at the main station.

Season	South top	South middle	South bottom	North top	North middle	North bottom
Early spring						
A ₁	25.0	22.6	19.6	23.0	22.5	19.8
A ₂	7.8	8.7	11.0	14.2	12.2	9.9
Late spring						
A ₁	22.8	21.5	20.0	23.4	20.0	20.3
A ₂	8.0	9.1	9.8	13.2	8.8	8.3
Early summer						
A ₁	19.9	18.8	16.4	17.9	20.8	23.4
A ₂	7.6	8.5	8.0	9.7	8.0	9.4
Mid-summer						
A ₁	8.7	8.4	8.9	9.1	12.8	15.5
A ₂	4.8	4.7	4.1	5.2	6.0	5.7
Late summer						
A ₁	20.7	16.9	17.2	16.7	20.2	19.1
A ₂	5.0	5.2	5.9	6.2	4.8	7.5
Early fall						
A ₁	8.8	7.4	10.1	7.5	11.4	12.3
A ₂	3.6	3.1	2.8	3.6	3.5	3.7
Late fall						
A ₁	31.8	25.0	24.3	25.9	33.5	42.4
A ₂	10.8	9.2	10.1	23.0	10.5	12.4

bottom of the north slope (Fig. 8) showed a further difference between the soil-moisture regimes of the slopes obscured by the seasonal, or even weekly, averages. During late spring and early summer four well-developed cycles of wetting and drying (A, B, C, and D) occurred at the top of the south slope. These cycles were poorly developed at the bottom of the north slope. There was one cycle of drying during summer and one in fall. These extended cycles, marking the periods of summer and fall drought, occurred on both slopes but were more severe on the south slope. Thus, even during late spring and early summer, when soil-moisture levels were the most favorable of any season, repeated cycles of drying took place on the south slope. These cycles of high moisture stress, developing in response to periods of low rainfall and high temperature, probably were a significant habitat difference between the slopes.

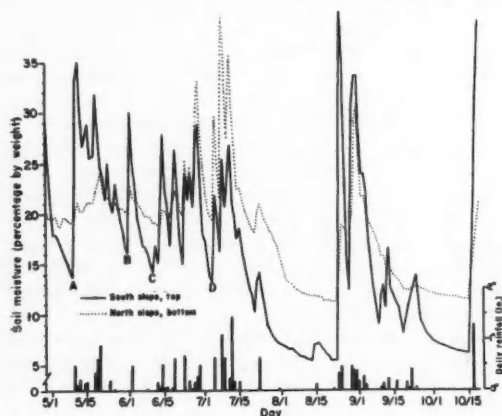


FIG. 8. Daily mid-afternoon soil moisture in A_1 horizon at top of south slope and bottom of north slope at main station (from Cooper 1960a).

Soil-moisture regimes in the A_2 horizon operated through a smaller range and fell much lower during dry periods than did soils of the A_1 horizon. The high values of early spring were never fully re-

plenished until the heavy rains of fall after the end of the growing season. Variations in intensity, interception by the canopy and litter, and retention of water in the surface layers of the soil combined to limit the effectiveness of summer rains in wetting the A_2 horizon. For example, a heavy rain (0.65 in.) fell during the morning of July 22. Moistures in the A_1 horizon were raised more than 20% at several stations, but in the A_2 horizon the greatest increase was 2.4% and several stations showed no increase at all. During the second and third weeks of September there was no moisture increase in the A_2 horizon despite 4 moderate rainfalls and 2 showers. Moisture was lost continuously through the 2-week period while 3 cycles of wetting and drying took place in the A_1 horizon. Thus, plants having their major root activity in the A_2 horizon must be able to operate on a low moisture budget throughout most of the growing season. As mentioned, the effects of this lower moisture budget were not as great on north slopes.

SUMMARY OF MICROCLIMATES

The major differences between the microclimates of the slopes are summarized (Table 12) by average values for major microenvironmental factors for the period March 31–September 14, 1957 (the period of most intensive instrumentation).

Most of the differences between the slopes may be related to basic differences in their solar radiation budgets. Differences in visible radiation (relative light intensity) may be taken as indications of differences in total solar radiation budgets (Table 12). Relative light intensity was greatest on south slopes, averaging over 5% higher than on north slopes. Furthermore average intensities were highest at the top and middle of the south slope (21.8% and 21.5%) and diminished to a low of 9.3% at the bottom of the north slope.

The greater net solar radiation budget of the south slopes, interacting with vegetation, produced higher air and soil temperatures, higher evaporation rates, and lower soil moisture values on south slopes than on north slopes (Table 12). Average air temperatures were higher on south slopes throughout most of the year and different maximum air temperature

TABLE 12. Averages of weekly values for principal microenvironmental factors at scattered and main stations, March 31–September 14, 1957.

Factor	SCATTERED STATIONS		MAIN STATION					
	South slopes	North slopes	South top	South middle	South bottom	North top	North middle	North bottom
Relative light intensity (%)	15.6	10.3	21.8	21.5	18.8	11.3	10.5	9.3
Maximum air temp., 50 cm (°F)	81.8	75.0	73.2	72.9	72.9	72.0	71.7	71.6
Maximum air temp., 10 cm (°F)	83.5	75.6	81.9	80.7	80.2	75.9	74.4	75.3
Minimum air temp., 50 cm (°F)	51.3	50.7	51.8	52.0	51.6	51.6	52.3	51.5
Minimum air temp., 10 cm (°F)	52.3	51.5	54.7	54.6	54.2	54.5	53.4	53.2
Evaporation (cc)	*	*	113.4	112.3	101.3	81.9	75.0	66.7
Soil temp., A_1 (°F)	65.9	61.9	67.6	67.0	64.8	60.0	59.8	57.9
Soil temp., A_2 (°F)	61.3	56.9	61.3	60.6	59.3	56.4	55.9	55.2
Soil moisture, A_1 (% by weight)	14.5	19.6	15.1	13.0	13.0	15.3	16.4	18.2

* Not sampled.

regimes characterized the slopes. Maximum air temperatures averaged almost 7° higher at 50 cm and 8° higher at 10 cm on south slopes at the scattered stations. Average maxima at both levels at the main station were highest at the top of the south slope and declined to lows at the middle and bottom of the north slope. Soil temperatures in the A₁ horizon averaged 4° higher on south slopes at the scattered stations and such temperatures averaged almost 10° higher at the top of the south slope than at the bottom of the north slope at the main station. Similar differences were observed in the A₂ horizon. Evaporation rates at the main station averaged 50-70% greater on the south slope than at the bottom of the north slope. Soil moisture levels were somewhat variable, but in general average values were lower on south slopes than on north slopes.

In summary, the microclimates varied from warm and dry, with relatively wide extremes, on south slopes, to cooler, more moist, and less variable on

north slopes. Whereas south slopes had a xeric microclimate, north slopes were more mesic. Furthermore, xeric characteristics were best expressed at the top of south slopes and more mesic conditions were best expressed at bottoms of north slopes. Stations topographically intermediate between these extremes showed correspondingly intermediate microclimates.

The data suggested that the microclimates studied constituted a microenvironmental gradient. That such a gradient exists can be shown by the use of scatter diagrams (Fig. 9). In these diagrams topographic and vegetational features are used for the graph axes. Each point represents a station sampled and the radiating lines represent 8 major environmental factors. The length of each line is determined from the range of values of the yearly averages for each factor. The shortest line represents a value in the lowest 1/4 of the range with lengths increasing for values in the second, third, and highest quarters. Soil moisture values are reversed, with low soil moisture values being placed in the highest quarter and high values in the lowest.

These figures show that the north slopes are characterized by predominantly short radiating lines whereas south slopes have long lines for almost every factor. At the main station, the bottom of the north slope has all short radiating lines indicating low (or narrow) yearly averages. The number of long lines, indicating increasing xerism, increases up the north slope and also up the south slope with the middle and top of the south slope having almost all long lines. Thus, the method gives a visual representation to the variation in the microclimates in addition to indicating their gradient relationships.

RESULTS: VEGETATION³

Just as a knowledge of the regional climate is necessary for an interpretation of specific microclimates, the regional biological spectrum is basic to an understanding of variations in community life-form composition. The biological spectrum for the entire Reserve flora was hemicryptophytic, as were spectra for other communities on the Reserve, in that they showed an increase of over twice the number of hemicryptophytes and cryptophytes in the normal spectrum at the expense of phanerophytes and chamaephytes (Table 13). Such spectra are characteristic of temperate regions with an unfavorable season represented by a cold winter. Differences between field and forest communities with respect to percentages of phanerophytes, hemicryptophytes, and therophytes merely reflect differences in the physiognomy of these types. Cryptophytes were less important in the upland areas than in the total flora because of the absence of hydro- and helophytes in these habitats.

The greatest differences in vegetation at the study sites were found in a comparison of the grouped slopes (see page 18). Because of the limited num-

³ For the raw data and other vegetational correlations see Cooper, 1958.

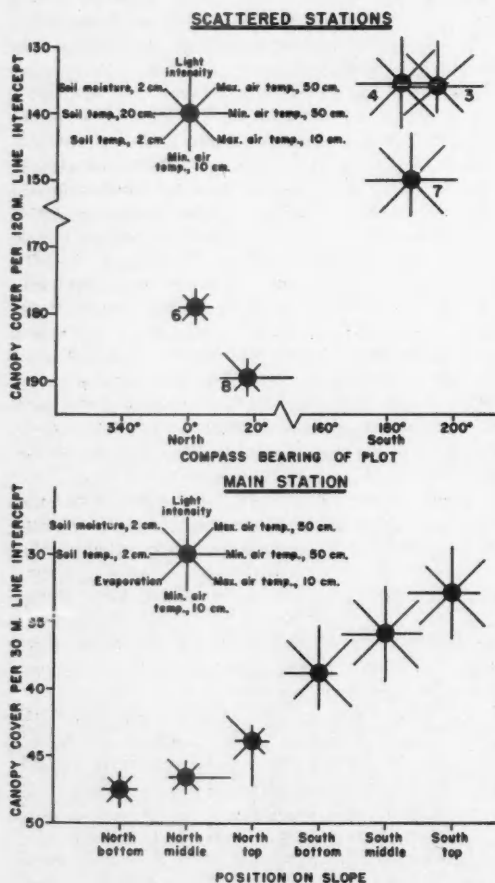


FIG. 9. Scatter diagrams showing relationships between slope and slope position, canopy cover, and microclimatic averages at scattered and main stations. See text for explanation.

TABLE 13. Presence-based life-form spectra for certain upland communities on the E. S. George Reserve.

Community	No. spp.	Ph	Ch	H	Cr	Th
<i>Total Reserve flora</i> (Cooper, 1958).....	567	16.5	1.4	56.0	15.0	11.1
<i>Old field</i> (Evans and Cain, 1952).....	90	8.9	2.2	64.5	11.1	13.3
<i>Upland forest</i> (Cooper, 1958)						
West Woods.....	100	30.0	1.0	55.0	13.0	1.0
Southwest Woods.....	97	33.0	0.0	51.5	14.5	1.0
Big Woods.....	219	23.2	1.8	59.8	11.4	4.6
<i>Normal Spectrum</i> (Raunkiaer, 1934).....	1000	46.0	9.0	26.0	6.0	13.0

bers of slopes in each group, statistical comparisons were not made. Only the most evident differences are discussed. Stations 12 and 13 were eliminated from these comparisons as their central tiers contained old roadways and thus were somewhat disturbed.

There were several gross vegetational differences between the groups of slopes. Despite the fact that there were no great differences in total numbers of species within the groups, the total number of hemi-cryptophyte species was lowest on protected north slopes (53) and open north slopes (55) increasing to 56 on protected south slopes and 59 on open south slopes. Phanerophytes were most numerous on both protected north slopes and protected south slopes (31 on each) and least abundant on open north slopes (27) and open south slopes (26). Total vegetative cover was greatest on protected north slopes, averaging 21,767 cm/120 m, diminishing to 20,153 cm on open north slopes and 19,729 cm on protected south slopes. Total cover was least on open south slopes, averaging 17,826 cm/120 m. Of this total cover, by far the greatest percentage was phanerophytic. Phanerophyte cover values were greatest on protected north slopes (20,480 cm/120 m), diminishing to 17,960 cm on open north slopes and 17,831 cm on protected south slopes, and were least on open south slopes (14,810 cm).

There were also differences in the field layers of the grouped slopes. Total field layer cover averaged 3064 cm/180 m on protected north slopes, increasing to 4158 cm on open north slopes, 5305 cm on protected south slopes, and 6427 cm on open south slopes. Total hemi-cryptophyte cover was lowest (967 cm/180 m) on protected north slopes and averaged 3 times as great (2974 cm) on open south slopes. Open north slopes and protected south slopes had intermediate values. Field layer phanerophyte cover averaged least (894 cm/180 m) on open north slopes and most on protected south slopes (2472 cm). Values on protected north slopes and open south slopes were 1202 cm and 1925 cm respectively.

Certain variations within life-form subclasses were also evident. Canopy cover (total cover of meso- and megaphanerophytes) averaged 175 m/120 m on protected north slopes, 159 m on open north slopes, 158 m on protected south slopes, and 135 m on open south slopes. Comparable basal areas for the grouped

slopes were 26.2, 26.7, 20.6, and 21.4 ft²/900 m². Total microphanerophyte cover also was greatest on protected north slopes (21.8 m/120 m) and least on open south slopes (0.4 m). Values on open north slopes and protected south slopes were intermediate, being 14.5 m and 3.6 m respectively. Among hemi-cryptophytes, protohemi-cryptophytes had, on the average, 10 times greater cover value on open south slopes than on protected north slopes. Rosette hemi-cryptophyte cover was greatest on open north slopes (349 cm/180 m) and protected north slopes (331 cm), diminishing to 66 cm on protected south slopes and 37 cm on open south slopes. There were no clear patterns with respect to distributions of true nanophanerophytes, chamaephytes, geophytes⁴ and therophytes.

The differences in field layer life-form distributions suggested that there might also be shifts in life-form dominance from the bottoms to the tops of the grouped slopes. As each plot consisted of 3 tiers of 3 100 m² plots, data were available from the top, middle, and bottom of each slope. From these data trends in life-form composition at different slope positions were analyzed.

Each group of slopes had a characteristic distribution of field-layer life-forms. On protected north slopes total cover in the field layer increased toward the slope tops. Relative cover of hemi-cryptophytes was greatest in the middle of the slopes where relative values of geophytes and nanophanerophytes were least. Geophytes and hemi-cryptophytes were of about equal importance at the bottoms of these slopes and hemi-cryptophytes increased in relative value upslope. Open north slopes showed an opposite pattern, total field-layer cover decreasing toward slope tops. Hemi-cryptophytes were of greatest relative importance at the slope bottoms and decreased in importance upslope, whereas geophytes and nanophanerophytes had greatest relative values at slope tops and decreased in importance downslope. Thus, the 2 groups of north slopes showed almost reverse trends.

On open south slopes field-layer cover increased greatly toward slope tops. Hemi-cryptophytes had almost twice the relative value at the tops of the slopes as at the bottoms and nanophanerophytes decreased in importance toward the slope tops. Geophytes had rather constant relative coverage but decreased upslope in relation to hemi-cryptophytes. Protected south slopes showed the same general trends, but in a less marked fashion.

From these data it is possible to generalize that, within the field layer, in situations where hemi-cryptophytes increase in relative importance geophytes and woody field-layer species decrease.

Despite differences in degree of protection afforded the slopes and variations in topographic outline it was possible to demonstrate certain contrasts between all north slopes as opposed to all south slopes. Distribution of species in life-form classes and presence-

⁴ As geophytes were the only class of cryptophytes represented, the term geophyte is used when referring to the cryptophyte life-form.

based life-form spectra showed that there were no significant (Mann-Whitney U Test, Siegel 1956) differences between the distribution of life-forms in the total floras of the north and south slopes. There were slightly more species on south slopes, an average of 105 to 102. There was an average of 30 phanerophytes on north slopes and 27 on south slopes. Hemipterophytes were more numerous on south slopes, an average of 60 to 54. However, the wide ranges in the values negated these small differences.

Analysis of total cover values for each life-form class (Fig. 10) and coverage-based life-form spectra for the entire plot vegetation showed that there were differences in the importance of certain life-forms on the slopes. There was a significantly greater total vegetative cover (5% level) and cover of phanerophytes (5% level) on north slopes and a significantly greater cover of hemipterophytes (1% level) on south slopes. There were no significant differences in the distribution patterns of other life-form classes.

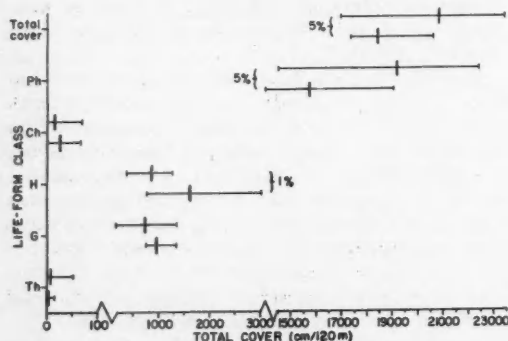


FIG. 10. Total cover of each life-form class in total vegetation of slopes. Upper line of pair indicates north slopes, lower line south slopes. Horizontal line indicates the range of values and vertical bar the mean value. Percent values refer to significance levels using the Mann-Whitney U Test (Siegel 1956). Ph=phanerophytes; Ch=chamaephytes; H=hemipterophytes; G=geophytes; Th=therophytes.

Spectra constructed from the total flora of sample plots, however, are too general to be sensitive. They include members of different strata which, in maturity, are responding to different sets of microenvironmental factors. Cantlon (1953) showed that vegetational differences between slopes, in conjunction with microclimatic differences, increased with proximity to the soil surface. Thus, an analysis of the field-layer (forest floor) vegetation, which is established under, and responds to, the microclimatic conditions near the ground, should yield the greatest differences between the structure of the vegetation of the slopes. In addition, when studies exclude the tree layer and are based on coverage, the overwhelming influence of the trees is escaped and other differences become more apparent.

There were no significant differences either in distribution of species in life-form classes or in presence-based life-form spectra for the slope field layers. The distributions and spectra were virtually identical to those for total plot floras as almost all canopy and understory species were represented by reproduction in the field layer.

However, total cover values for each life-form class (Fig. 11) and coverage-based life-form spectra showed that there were differences between the slopes. There was a significantly greater total field-layer cover (1% level), cover of nanophanerophytes (5% level) and hemipterophytes (1% level) on south slopes. There were no significant differences with respect to cover of chamaephytes, geophytes, or therophytes.

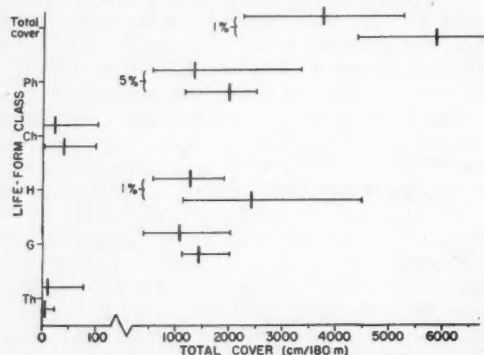


FIG. 11. Total cover of life-form classes in field-layer vegetation. Explanation and abbreviations as in Fig. 10.

Thus, the gross structure of the vegetation on the slopes was different. On the north slopes there was a greater total plant cover and cover of phanerophytes (trees and shrubs) but a more poorly-developed field layer. On the south slopes there was less tree and shrub cover but greater field-layer cover. Within the field layer, cover of nanophanerophytes and hemipterophytes was greater on south slopes than on north slopes.

Analysis of the distribution patterns of the subclasses of the 5 major life-form classes brought out further differences between the slopes. Among phanerophytes (Fig. 12), there was a significantly greater diversity of species and significantly greater cover (1% level) of meso- and megaphanerophytes on north slopes. Breakdown of data for trees (meso- and megaphanerophytes) showed that although there were no differences in total number of stems or in stems of smaller size classes (Table 14), there were significantly more large trees (over 18 in. d.b.h.) on north slopes. The total basal area averaged 5 ft more per 900 m² on the north slopes and this difference was significant at the 1% level. The tree of mean diameter was also significantly larger (5% level) on the north slopes. Although there was no significant difference in the number of microphanerophyte species or stems on the slopes, this life-form had a somewhat

significantly greater cover on north slopes (10% level). There was great variability in the distribution of microphanerophytes on north slopes as the deviations in Figure 12 indicate. The heavy cover at several stations (1, 10, 11) was produced by a dense growth of *Hamamelis virginiana* whereas on other north slopes cover was contributed by more widely-spaced saplings, small trees, and *Hamamelis*. On south slopes cover was uniformly low and was mostly of scattered saplings and individuals of *Amelanchier*.

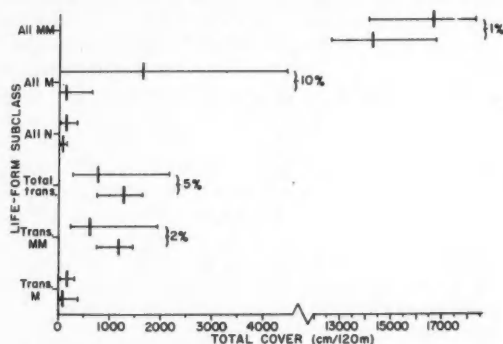


FIG. 12. Total cover of phanerophyte subclasses. Explanation as in Fig. 10. MM=meso- and megaphanerophytes; M=microphanerophytes; N=nanophanerophytes.

TABLE 14. Density and basal area (per 900 m²) of meso- and megaphanerophytes.

Plot	Total stems over 1 in. d.b.h.	Stems over 18 in. d.b.h.	Basal area (ft ²)	Tree of mean diam. (in.)
<i>North slopes</i>				
1.....	70	2	30.7	9.0
6.....	62	4	26.4	9.0
8.....	83	4	27.5	7.7
10.....	49	3	22.9	9.4
11.....	57	0	23.4	8.7
13.....	73	1	23.3	7.6
15.....	48	4	29.1	11.0
16.....	105	3	24.7	6.6
Mean.....	68	2.6 ^a	26.0 ^b	8.6 ^c
<i>South slopes</i>				
2.....	71	1	21.7	7.6
3.....	82	0	19.2	6.6
4.....	74	0	18.8	7.0
7.....	80	0	20.8	6.9
9.....	95	0	24.0	6.8
12.....	62	1	19.7	8.0
14.....	67	1	20.3	7.4
17.....	62	2	23.3	8.4
Mean.....	74	0.6 ^a	21.0 ^b	7.3 ^c

^a Difference significant at 2% level.

^b Difference significant at 1% level.

^c Difference significant at 5% level.

Other difference not significant.

Of the field-layer phanerophytes (Fig. 12), some were true nanophanerophytes and thus natural elements of the field layer whereas others were trans-

gressives which eventually will exceed the nanophanerophyte class. There was no significant difference in the number of species or total cover of true nanophanerophytes on the slopes. As the small cover values indicate, this life-form was not significant in the total field-layer vegetation. However, cover of all transgressives was significantly greater on south slopes. Breakdown of this phanerophyte reproduction showed the source of difference to be within reproduction of the meso- and megaphanerophyte classes. These life-forms had significantly greater cover (2% level) on south slopes whereas there was no significant difference in cover of microphanerophyte reproduction. Thus, whereas conditions favored germination and establishment of tree reproduction on south slopes, conditions on north slopes appeared to be such that a greater number of individuals reached maturity and those that matured grew to larger sizes. Mortality on south slopes seemed to occur between the seedling and sapling stages.

Analysis of the herbaceous element of the field layer showed further differences between the slopes (Fig. 13). There were greater numbers of protohemipterophytes and these had a significantly greater cover value (1% level) on south slopes. There were no significant differences, either in number of species or cover, of semi-rosette hemipterophytes. However, rosette hemipterophytes had significantly more cover (1% level) on north slopes. Thus, the differences between the hemipterophyte populations of the slopes are due to the considerably greater dominance of protohemipterophytes on south slopes.

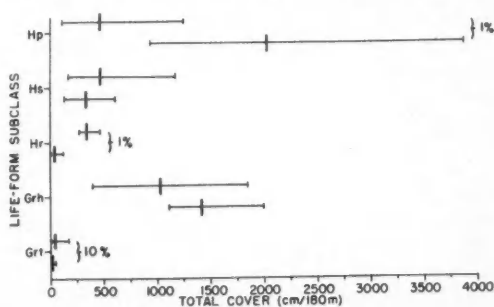


FIG. 13. Total cover of hemipterophyte and geophyte subclasses. Explanation as in Fig. 10. Hp=protohemipterophytes; Hs=semi-rosette hemipterophytes; Hr=rosette hemipterophytes; Grh=rhizome geophytes; Grt=root tuber geophytes.

There were no great differences in the number of species or cover values of geophytes, chamaephytes, or therophytes. Although there was no significant difference in total geophyte or rhizome geophyte cover, there was a somewhat significantly greater cover (10% level) of root-tuber geophytes on north slopes. As only 2 species were involved, this relationship seems of questionable importance. Only 4 chamaephytes were encountered in this study and, in terms of coverage, these were an insignificant component of the

vegetation. This is in keeping with other life-form studies of eastern American deciduous forest. Therophytes were irregularly distributed and were not found to be more important on south slopes, either in number of species or cover. Other workers (Oosting 1942, Cantlon 1953, Miller & Buell 1956) found more therophytes on south than north slopes and related this condition to the lack of light and open ground on north slopes. Although there often were more therophytes in stands with low canopy cover this relationship was by no means consistent. Their presence seemed more related to available disturbed or open ground, regardless of slope orientation.

As previously indicated, there are few studies dealing with the distribution of Raunkiaerian leaf-size classes within a single vegetation type. The data of this study offered an opportunity to analyze variation in distribution of leaf-size classes within a large community and to relate this variation, where possible, to habitat variation.

Analysis of leaf-sizes in the Big Woods showed that 58% of the species were microphylls. Nanophylls (19.7%) and mesophylls (18.4%) were of secondary importance and the larger-sized leaves, macrophylls and megaphylls, were absent. Other woodland communities on the Reserve showed very similar patterns. These distributions were similar to those of other deciduous forests and to that reported for temperate gallery rain forest by Cain *et al.* (1956). There was a definite shift toward a greater percentage of small leaves, leptophylls and nanophylls, in the old-field community studied by Evans & Cain (1952).

Analysis of the entire plot vegetation showed several differences in leaf-size classes on the slopes. On a species basis, only differences in presence of nano-

phylls were significant, as this size class was more abundant on south slopes. However, total cover (Fig. 14, top) of leptophylls and microphylls was significantly greater (1% level and 10% level respectively) on south slopes. Total cover of mesophylls was significantly greater (2% level) on north slopes. The greater mesophyll cover on north slopes was directly related to the greater tree dominance on those slopes as virtually all trees had mesophylls. Although there were significantly more nanophyllous species on south slopes, there were no differences in cover values for this class.

Proportions in the field layer were somewhat different. Here leptophylls, microphylls, and mesophylls all had significantly greater cover (1%, 2%, and 10% levels respectively) on the south slopes (Fig. 14, bottom). The greater cover of mesophylls in the field layer on south slopes as opposed to their greater coverage in the total vegetation of north slopes was related to the similar shift in dominance of phanerophytes. The greater cover of mesophylls in the field layer on south slopes was due to the greater cover of transgressives on the south slopes, as these transgressives were virtually all reproduction of the mesophyll-class trees.

Those life-forms confined to the herbaceous synusia (Fig. 15) had a more definite pattern of difference between the slopes. Among these species, leptophylls and microphylls again had significantly greater cover on south slopes (both 1% level). However, herbaceous mesophylls had significantly greater cover (1% level) on north slopes. Thus, there was a greater importance of herbaceous species with small leaves on south slopes whereas herbaceous species with larger leaves were a more prevalent element on north slopes.

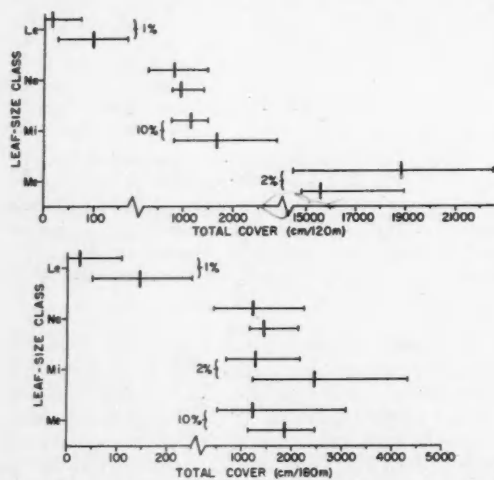


FIG. 14. Total cover of leaf-size classes in total vegetation (above) and field-layer vegetation (below). Explanation as in Fig. 10. Le=leptophylls; Na=nanophylls; Mi=microphylls; Me=mesophylls.

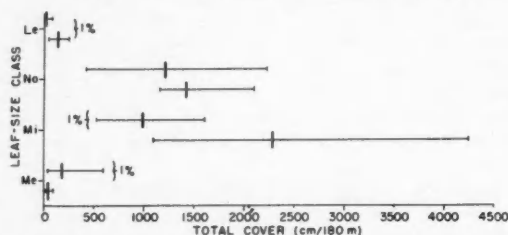


FIG. 15. Total cover of leaf-size classes among herbaceous species. Explanation as in Fig. 10, abbreviations as in Fig. 14.

There were no great variations in dominance of leaf-size classes at different slope positions. Leptophyll cover averaged the least at the bottoms of the north slopes and the most at the tops of the south slopes. These trends, however, were not significant. Herbaceous mesophylls showed a reverse pattern, having the greatest cover at bottoms of north slopes, but these trends also were not significant. Microphyll cover increased up the north slope and was significantly greater (10% level) at the top of the south slope than at the bottom.

RELATIONSHIPS BETWEEN LIFE-FORMS AND MICROCLIMATE

Several approaches to the interrelations of vegetational and microclimatic data were possible. The most direct was correlation of variations in life-form distribution with variations in single factors of the microclimate. However, as the variations in light, air and soil temperature, evaporation, and soil moisture formed a gradient of change from a mesic to a xeric extreme, each vegetational feature would show the same general relationships with each of the individual microclimatic factors. Thus, another approach seemed desirable.

As the presence of a plant on a given site is generally determined by a complex of environmental factors rather than by one factor alone (Billings 1952), the differences in vegetation between sites (on a compositional or structural basis) may be regarded as due to the sum of the environmental differences between the sites. Thus, a method which gathered together the differences in the several environmental features at each site and expressed these as one cumulative value seemed a logical means of expressing the total environmental differences among the sites studied.

Such a combination of data, termed the Microenvironmental Index, was used in this study. The Index was computed in the same manner as a Hybrid Index (Anderson 1949). Base figures used in computation were averages for environmental factors for the period March 31 to September 14, 1957. A total range of 10 was used, with mesic features such as low light intensities, low temperatures, low evaporation rates, and higher soil moistures assigned values near zero and xeric features assigned values near 10. In assigning final values, the mesic extreme of a given factor was assigned a value of 0 and the xeric extreme a value of 10. Intermediate values were placed along a scale in their proper position between the extremes and assigned Index values by comparison with the scale of 10 equal units. Ten factors for each set of data were used, making a total possible Index range from 0-100. Thus, values near 100 indicated xeric microenvironments whereas values near zero indicated more mesic conditions.

Microenvironmental Indices for both the scattered and main stations are shown in Table 15. At the scattered stations high Indices were characteristic of the south slopes and lower values occurred on the north slopes. At the main station Indices were highest at the top of the south slope and declined to a low at the bottom of the north slope. These values corresponded very closely to the positions of the dots in the scatter diagrams (Fig. 9) and offered a sort of numerical corroboration of the conclusions drawn from them.

Several limitations exist on the data available for comparison. Indices for the scattered and main stations cannot be compared because of the differences in the types of instrumentation (maximum tempera-

TABLE 15. Computation of Microenvironmental Indices for scattered and main stations.

A. Scattered Stations	SOUTH SLOPES			NORTH SLOPES		
	3	4	7	5	6	8
Max. Air Temp., 50 cm....	8.8	10.0	7.7	0.5	1.1	0.0
Min. Air Temp., 50 cm....	8.6	10.0	8.1	6.3	0.0	10.0
Range, Air Temp., 50 cm....	9.0	10.0	7.8	1.7	2.8	0.0
Max. Air Temp., 10 cm....	7.0	10.0	9.8	0.0	0.5	1.0
Min. Air Temp., 10 cm....	3.6	10.0	5.7	0.0	0.4	2.2
Range, Air Temp., 10 cm....	6.6	9.0	10.0	0.0	0.5	0.2
Light Intensity.....	8.8	10.0	8.0	3.0	0.0	1.2
Soil Temp., 2 cm.....	8.8	10.0	9.8	0.0	0.8	2.4
Soil Temp., 20 cm.....	9.5	10.0	8.7	0.9	0.0	3.0
Soil Moisture, 2 cm.....	7.7	6.8	10.0	0.0	2.3	5.2
Microenvironmental Index.	78.4	95.8	85.6	12.4	8.4	25.2

B. Main Station	SOUTH SLOPE			NORTH SLOPE		
	Top	Middle	Bottom	Top	Middle	Bottom
Max. Air Temp., 50 cm....	10.0	8.1	8.2	2.2	0.6	0.0
Min. Air Temp., 50 cm....	4.2	6.0	1.0	0.8	10.0	0.0
Range, Air Temp., 50 cm....	9.3	8.1	10.0	5.4	0.0	8.4
Max. Air Temp., 10 cm....	10.0	8.5	7.9	2.2	0.0	1.2
Min. Air Temp., 10 cm....	10.0	9.0	6.3	8.5	1.6	0.0
Evaporation.....	10.0	9.8	7.4	3.2	2.2	0.0
Light Intensity.....	10.0	9.6	7.5	1.7	0.9	0.0
Soil Temperature, 2 cm....	10.0	9.4	6.9	2.2	2.0	0.0
Soil Temperature, 20 cm....	10.0	9.0	6.7	2.1	1.0	0.0
Soil Moisture, 2 cm.....	6.1	10.0	9.9	5.6	3.3	0.0
Microenvironmental Index.	89.6	87.5	71.8	33.9	21.6	9.6

ture, e.g.) and in factors recorded (evaporation at the main station only). Furthermore, the north slope at the main station was a protected north slope and the south slope was an open slope. Thus, any correlations of microclimatic data for different slope positions with vegetational changes were limited to correlations of vegetational data from protected north slopes and open south slopes with microclimatic data from the main station.

Gross vegetational features correlated rather well with the Microenvironmental Index. Total field layer cover increased greatly in the more xeric microenvironments. Field layer cover averaged 3064 cm and 4158 cm on protected and open north slopes respectively, increasing to 5305 cm on protected south slopes and 6427 cm on open south slopes. Total cover also increased from an average of 696 cm at the bottom, to 1174 cm at the middle, and 1193 cm at the top of protected north slopes and from 1765 cm at the bottom of open south slopes to 2135 cm and 2527 cm at the middle and top of these slopes.

Relative cover of hemieryptophytes (Table 16) showed a general increase in more xeric microclimates. Although the variations at the extremes were considerable, intermediate stations showed some deviations. Relative cover of geophytes (Table 16) appeared to be greatest in areas with low Index values (mesic) and to decrease as Index values increased. The variation at the extremes, however, was not as great as with hemieryptophytes. Thus, although the

TABLE 16. Relative coverage of herbaceous life-forms in relation to Microenvironmental Indices on grouped slopes. H=hemipterophytes; G=geophytes; Le=leptophylls; Mi=microphylls; Me=mesophylls; MiH=hemipterophytes with microphylls; MeG=geophytes with mesophylls.

Station	Index* value	RELATIVE COVERAGE OF:						
		H	G	Le	Mi	Me	MiH	MeG
Protected north slopes	10.4	35.3	25.8	0.1	51.2	7.0	45.8	3.3
Open north slopes	25.2	42.3	34.5	0.9	34.9	8.8	30.9	1.4
Protected south slopes	85.6	27.5	24.4	1.6	48.7	3.1	46.8	1.3
Open south slopes	87.1	45.9	23.4	4.5	62.1	0.8	60.1	0.3
Protected north slopes								
Bottom	9.6	26.7	27.5	0.0	54.0	10.0	45.8	8.4
Middle	21.6	44.2	23.8	0.1	59.2	6.5	54.8	2.9
Top	33.9	33.6	26.5	0.1	43.1	6.5	38.7	1.7
Open south slopes								
Bottom	71.8	28.2	21.8	7.0	53.2	1.6	51.4	0.9
Middle	87.5	44.9	28.0	3.7	57.3	0.4	56.4	0.2
Top	89.6	57.4	21.3	4.6	68.0	0.9	64.8	0.1

* Index values from Table 15.

patterns were by no means linear, relative cover of hemipterophytes and geophytes showed more or less reverse trends with values for hemipterophytes greatest on xeric sites and those for geophytes greatest on more mesic sites.

Herbaceous leaf-size classes also showed variations in relation to shifts in microclimate (Table 16). Relative coverage of herbaceous leptophylls and microphylls increased with higher Index values whereas relative coverage of herbaceous mesophylls was greatest in sites with lower Index values. These changes were evident both in data from the grouped plots and in data showing variation with slope position. Again, although the relationships were not linear, the trends and the variations at the extremes were clear.

In summarizing, there was a trend toward a lower relative coverage of geophytes and herbaceous plants with mesophylls as microclimates became more xeric. Hemipterophytes and plants with leptophylls and microphylls increased in relative coverage as microclimates became more xeric.

These generalizations are shown by the fact that relative coverage of geophytes with mesophylls decreased in xeric microclimates (Table 16). Relative coverage of microphyllous hemipterophytes showed a reverse trend, increasing on xeric sites. These variations showed less irregularity than did relationships between Index values and entire life-form or leaf-size classes.

Data as yet undiscussed suggest another approach which is of interest not only in this study but also on a wider basis within the deciduous forest formation. In southeastern Michigan and nearby areas, mesic forests (usually the Beech-Maple type) are characterized by an herbaceous stratum in which the hemipterophyte and geophyte life-forms are of almost equal importance. In the most mesic situations this equality may be demonstrated on a species-presence basis whereas on a coverage basis geophytes may out-

rank hemipterophytes in importance, particularly in spring. The more xeric environments (Oak-Hickory woodlands, for example) have a much greater number of hemipterophytes with geophytes constituting a minor portion of the vegetation. These generalizations are supported by life-form spectra from several regional forest communities (Table 17) which show a progression in presence-based spectra from an approximate 1:1 ratio of hemipterophytes to geophytes in the Beech-Maple forest to a ratio of about 5:1 in the Oak-Hickory stand. Frequency-based spectra from the same communities showed similar trends.

TABLE 17. Presence-based life-form spectra for field-layer vegetation from various communities showing variation in hemipterophyte:geophyte ratio.

Community and location	Ph	Ch	H	G	Th	H/G ratio	Author
Beech-Maple	*	*	50.0	40.6	9.4	1.23	Esten, 1932
Turkey Run, Ind.							
Beech-Maple	42.9	1.4	28.6	22.9	4.3	1.25	Cain, 1935
Warrens Woods, Mich.							
Maple-Beech	26.6	0.0	40.0	30.0	3.3	1.33	Cain & Castro, 1950
Haven Hill, Mich.							
Oak-Hickory-Maple	*	*	54.6	36.4	9.1	1.50	Cooper, unpubl.
Ann Arbor, Mich.							
Oak-Hickory	23.2	1.8	59.8	11.4	4.6	5.20	Cooper, 1958
George Reserve, Mich.							

* Not sampled.

An example of succession in the deciduous forest region, from grassy fields to the *Aceretum* climax in the St. Lawrence lowland (Dansereau 1957), reveals a similar pattern. Here, the hemipterophyte:geophyte ratio decreased from 11.9 in the xeric consolidation *Poaetum*, to 7.0 in the *Solidaginetum*, 2.0 in the *Betuletum*, and 1.1 in the sugar maple climax forest. It is interesting to note that the *Aceretum saccharophori tsugosum* quasiclimax, which has a slightly lower hemipterophyte:geophyte ratio than the climax, is characterized by Dansereau as having narrower extremes of temperature and humidity than the climax.

Data adapted from Potzger & Friesner (1940) showed shifts in relative importance of hemipterophytes and geophytes on a seasonal basis in studies of the spring, summer and fall aspects of Beech-Maple and Oak-Hickory forests in southern Indiana. In the Beech-Maple woods, the hemipterophyte:geophyte ratio increased from 1.1 in spring, to 3.3 in summer, and 2.7 in fall. In the Oak-Hickory woods, the ratio was 2.7 in spring, 4.6 in summer, and 4.8 in fall. Thus, hemipterophytes were 2.5 times as important as geophytes, even in spring, in the drier Oak-Hickory forest.

From these data it appears that in the field layers of the most mesophytic deciduous hardwood stands, geophytes are of equal or greater importance than hemipterophytes. As the environment becomes more xeric hemipterophytes become increasingly dominant elements of the vegetation.

The data at hand offered an opportunity to test the ratio of hemipterophytes to geophytes (H/G ratio) against known microclimatic data. When average H/G cover ratios from the 4 groups of slopes were plotted against Index values from the scattered stations (Fig. 16), the relationships were not particularly close. There was an overall increase in the ratio from 1.65 on protected north slopes to 2.13 on open south slopes, but the other slopes showed lower ratios. Average ratios from the top, middle, and bottom of protected north slopes and open south slopes, plotted against Index values from the main station, showed a similar relationship at the extremes. The ratio was 0.97 at the bottom of protected north slopes, and 2.69 at the top of open south slopes. There was considerable variation between. In general, however, on north slopes geophyte cover values more closely approximated those of hemipterophytes. On south slopes, hemipterophytes were of greater relative importance.

The importance of microphylls on south slopes and

of mesophylls on north slopes suggested a refinement of the H/G ratio, termed the microphyllous hemipterophyte:mesophyllous geophyte ratio. When this ratio was plotted against Index values the results were more clear-cut (Fig. 17). Average values from the grouped slopes increased from 22.7 on protected north slopes to 756 on open south slopes. Values at the bottom of protected north slopes averaged 41.6, increasing up the slopes to a maximum value of 844 at the top of open south slopes. Thus, broad-leaved geophytes were of great importance on mesic north slopes and smaller-leaved hemipterophytes increased greatly in importance on the more xeric south slopes.

DISCUSSION

This study has shown that there are correlations between the distribution and importance of certain Raunkiaerian life-forms and small variations in local climate just as there are correlations between life-forms and the major climatic zones of the earth.

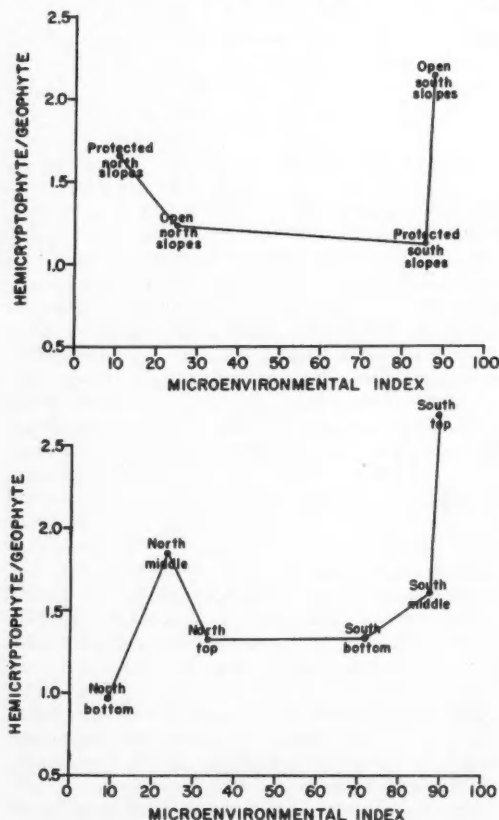


FIG. 16. Relationship between Microenvironmental Index and hemipterophyte:geophyte ratio on protected and open north and south slopes and at top, middle, and bottom of protected north and open south slopes. Index values from Table 15.

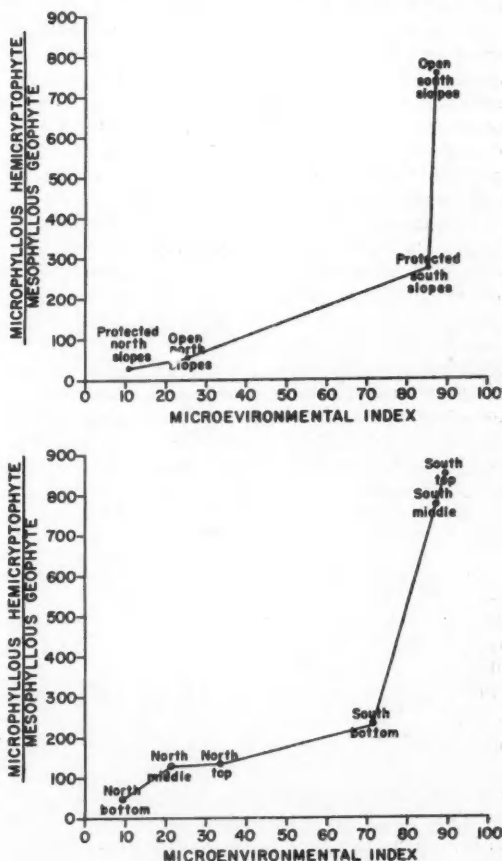


FIG. 17. Relationship between Microenvironmental Index and microphyllous hemipterophyte:mesophyllous geophyte ratio on protected and open north and south slopes and at top, middle, and bottom of protected north and open south slopes. Index values from Table 15.

The differences in life-form distribution in the Big Woods appeared to be less (both qualitatively and quantitatively) than might be expected in other types of vegetation and situations. The marginal site qualities and history of disturbance prevailing throughout most of the George Reserve combined to limit the development of a rich deciduous forest flora. It would be anticipated that similar studies elsewhere, particularly in undisturbed mesophytic forest areas, would reveal greater contrasts than those reported here.

The microclimatic data of this study emphasize the importance of topography as a factor in producing variations in forest "trunk space" microclimates. In general, the microclimates of the trunk space on north slopes were similar to those reported for dense or mature forests whereas comparable microclimates on south slopes resembled those of thin forests or open areas. These conclusions agree with those of Cantlon (1953) and the conclusions of similar studies (for which see Cantlon).

During most of the growing season the denser canopy and angle of slope combine to allow less solar radiation (as indicated by light regimes) to penetrate to the forest floor on north slopes. Only during early spring and the first weeks of late spring is the forest floor the active meteorological surface. The greatest daily and weekly ranges of temperature on north slopes occur during this period. These conditions are similar to those described for a dense Ohio beech forest (Christy 1952), for mesophytic forests in coves at Neotoma (Wolfe *et al.* 1949), and for oak-hickory forest in New Jersey (Sparkes & Buell 1955).

In contrast, south slopes received greater amounts of solar radiation throughout the entire growing season. Except in heavy shade, temperature stratification was, depending on the density of canopy, a weak to strong version of the incoming radiation type (Geiger 1957). Annual maxima here agreed more closely with maxima in the microclimate as was shown for thin oak forests on southwest-facing slopes at Neotoma (Wolfe *et al.* 1949).

The data also show the more favorable moisture relations of the trunk-space climate on north slopes. The higher solar radiation and temperature conditions produce evaporation rates on south slopes roughly 50% greater than those on north slopes. Potzger (1939) found a comparable situation on a ridge in Indiana. The percentage reduction of evaporation on north slopes found in this study approaches the difference between evaporation in forested and open areas (Kucera 1954, Selleck & Schuppert 1957).

Soil moisture values fluctuated less and did not fall as low on north slopes as on south slopes. Cantlon (1953) suggested that this was true for the north slope he studied in New Jersey. Recently, Gilbert & Wolfe (1959) have shown that soil moisture values on lower northeast-facing slopes under mixed mesophytic forest do not fall as close to the permanent

wilting point during summer droughts as do soils of southwest-facing slopes under mixed oak forest.

In view of the great microclimatic differences between the slopes the large differences in vegetation are not surprising. A comparison of these differences with those reported in other studies of the relations between life-forms and microclimate reveals certain similarities and differences.

Oosting (1942) and Cantlon (1953) showed that on the Piedmont of North Carolina and New Jersey phanerophytes and geophytes were more important elements of north slope floras as opposed to those of south slopes which were characterized by greater numbers of hemieryptophytes and therophytes. These conditions generally were true of the Big Woods on the George Reserve. Phanerophytes showed a greater dominance, both of the flora and vegetation, on north slopes whereas hemieryptophytes behaved similarly on south slopes. However, the studies of Oosting and of Cantlon dealt with the entire floras of the slopes and did not segregate the species by strata. In this study a treatment by strata showed that although meso- and megaphanerophytes had greater total cover values on north slopes their reproduction in the field layer was greater on south slopes.

On a world basis phanerophytes decrease in dominance with increasing climatic severity (generally extremes of temperature). This fact has been extended to the microclimatic level by Miller & Buell (1956) who concluded that in temperate regions a dominance of phanerophytes indicates a climate more "congenial" (showing less variation in extremes) for plant growth. The George Reserve data indicate that this is true only when the total vegetation of the slopes is considered. If the coverage of phanerophytes in the field layer of south slopes is compared with that of north slopes it might be concluded that the south slope microclimate was less variable in its extremes and thus was more favorable for plant growth. Such a conclusion is not warranted on the basis of the microclimatic data. Thus, statements that a dominance of phanerophytes indicates a microclimate with less variable extremes apparently are valid only in terms of the entire vegetation and not in terms of its component strata.

On a relative basis geophytes were more dominant on north slopes on the George Reserve. This fact is in agreement with the findings of Oosting (1942) and Cantlon (1953). However, Miller & Buell (1956) found that geophytes, on a coverage basis, were more important on south slopes near the prairie border region in Minnesota. They found this to be in accord with Raunkiaer's original hypothesis ascribing dominance of more-protected life-forms to those areas with the greatest climatic severity. There is a direct contradiction between these findings and those of the present study and of Oosting and Cantlon. In the deciduous forest region geophytes are more abundant (and dominant) in mesophytic forests characterized by greatly-moderated climatic extremes, whereas they are apparently more abundant on southwest-facing

slopes characterized by wide climatic extremes near the prairie-border region. Furthermore, it is interesting that there should be a greater geophyte dominance on southwest-facing slopes when, as Miller & Buell point out, such slopes immediately to the west show floristic and vegetational affinities to the hemicryptophytic grasslands lying even further west.

These problems emphasize the need for intensive regional studies of life-form behavior. They also emphasize the potential danger in generalizing about life-form behavior in relation to microclimate from a limited number of slope samples. The variability of the data encountered in this study of 16 slopes indicates that before meaningful generalizations can be made an even larger series of slopes should be sampled.

This study also shows the need for quantitative data in the evaluation of localized variations in life-form behavior. Few, if any, of the correlations presented can be made on the basis of species presence alone. The limited nature of the demonstrated changes emphasizes the desirability of quantitative evaluation of the importance of a particular life-form in a given situation and the potential usefulness of statistical analyses for determining the validity of apparent trends.

SUMMARY

A study of the relationships between Raunkiaerian plant life-forms and microclimate on north and south slopes in the Big Woods of the George Reserve in southeastern Michigan was conducted during 1957.

Microclimatic instrumentation was carried out on 3 north and 3 south slopes ("scattered stations") and at the top, middle, and bottom of the north- and south-facing sides of a hogback ("main station") in the Big Woods of the Reserve. Light intensity, air temperature, wind movement, evaporation, and soil temperature and moisture were sampled. Vegetational data were obtained from a series of 16 sample plots placed on well-exposed slopes which deviated not more than 20° from true north or south.

Relative light intensity was greatest on south slopes and intensities generally diminished downslope. Average air temperature was highest on south slopes and, except during early summer, average temperatures on south slopes increased toward the ground. On north slopes, maximum air temperatures and the greatest ranges in maxima occurred during the first weeks of late spring. On south slopes, maxima rose to a late spring peak, leveled off, and continued to rise to an annual mid-summer maximum. Summer maximum temperature ranges were greatest on south slopes. Minimum air temperatures showed less variation than maxima. During spring, minima were lower on north slopes and the greatest growing season range in minima at all stations occurred during spring. In summer, minima were similar on both slopes. Air movement was greatest at slope tops and diminished downslope. At times, air movement limited development of the incoming radiation type. Evaporation

was greatest at the top of the south slope and least at the bottom of the north slope. Soil temperatures were higher on south slopes throughout the growing season, with differences greatest in early spring. Annual maxima on both slopes were recorded in mid-summer. Differences between the slopes were least in late summer and fall. In winter, snow cover limited soil temperature fluctuations on north slopes but was seldom of any duration on south slopes. North slopes had higher soil moisture values than south slopes. Moisture was abundant on both slopes in spring but mid-summer and fall were seasons of soil moisture stress. On south slopes cycles of wetting and drying marked periods of adequate soil moisture whereas on north slopes these cycles were not as evident.

In summary, the microclimates of the slopes varied from a cool, moist (mesic) extreme at the bottom of north slopes to a warm, dry (xeric) extreme at the top of south slopes. Microclimatic conditions on north slopes resembled those of well-developed forests whereas those on south slopes were more similar to the microclimates of exposed areas.

The biological spectrum of the George Reserve was predominantly hemicryptophytic. Within the entire slope vegetation there was a greater phanerophyte cover on north slopes and hemicryptophyte cover on south slopes. In the field layer only, there was greater phanerophyte and hemicryptophyte cover on south slopes. There was a greater cover and basal area of meso- and megaphanerophytes on north slopes and a greater cover of microphanerophytes on north slopes. Transgressive nanophanerophytes had greater cover values on south slopes. Protohemiptophytes had greater cover on south slopes and rosette hemicryptophytes had greater cover on north slopes. Differentiation of plots into protected and exposed north and south slopes showed that within the field layer relative coverage of hemicryptophytes increased in situations where relative coverage of phanerophytes and geophytes decreased.

The flora of the George Reserve was predominantly microphyllous. Within the slope vegetation there was greater leptophyll and microphyll cover on south slopes and greater mesophyll cover on north slopes. Within the field layer, leptophylls, microphylls, and mesophylls had greater cover on south slopes. However, in the herbaceous element of the field layer mesophylls had more cover on north slopes whereas leptophylls and microphylls still had greater cover on south slopes.

Correlations between life-form and microclimatic data were confined to the field-layer vegetation. A Microenvironmental Index, expressing the sum of the environmental characteristics of a given site, was used for correlation with vegetational data. Total field layer cover and relative cover of hemicryptophytes was greatest in xeric microenvironments. Relative cover of geophytes was greatest in more mesic sites. Herbaceous leptophylls and microphylls increased in relative cover in xeric sites whereas her-

baceous mesophyll cover was greatest in mesic micro-environments.

Data from deciduous forest communities suggested that a low hemicryptophyte:geophyte (H/G) ratio was characteristic of mesic sites and that this ratio increases as the environment becomes more xeric. Comparison of the H/G ratio with Index values showed that, in general, low ratios were associated with mesic sites and high ratios with xeric sites. A similar, but closer, relationship was shown for the ratio of microphyllous hemicryptophytes to mesophyllous geophytes.

The microclimatic data obtained agree with those of other studies and emphasize the importance of topography as a factor producing variations in forest microclimates in that the microclimates of north slopes resembled those of mature forests whereas comparable microclimates on south slopes resembled those of thin forests or open areas. The life-form data are in agreement with those of other deciduous forest reports but disagree with an example from the prairie-deciduous forest transition. The data show the danger in generalizing concerning life-form and microclimate relations from limited numbers of slope samples.

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2. The second part of the report deals with the results of the work during the year. It is divided into two main sections: the first section deals with the results of the work during the year, and the second section deals with the results of the work during the year.

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EFFECTS OF COMPETITION, PREDATION BY *THAIS LAPILLUS*, AND OTHER FACTORS ON NATURAL POPULATIONS OF THE BAR- NACLE *BALANUS BALANOIDES*

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INTRODUCTION

This study represents an attempt to measure some of the major factors which affected the recruitment and mortality of a natural population of *Balanus balanoides* (L.) during a period of 2 2/3 years (1952-1955). Most emphasis was placed on the investigation of the effects of certain biological interactions such as intraspecific competition and predation by *Thais lapillus* L. (*Nucella*, *Purpura*; see Clench 1947 for synonymy). Other associated animals were studied, although in less detail; food and parasites were not studied. The size of the study area was purposely kept small in order to reduce the variability caused by differences in wave action, salinity, temperature, etc. Weather and tide records, however, afforded some information as to the effect of the physical factors of the environment. The results are presented as they occurred in the life of the barnacles, beginning with their attachment to the rock.

Barnacles possess certain advantages for this sort of study. The survival of individuals can be determined very accurately by simply mapping the posi-

tions of all the members of a group and then following the same individuals by regular censuses. As Deevey (1947) has pointed out, this method is as accurate as that used with laboratory populations, and is much superior to those methods which use the age at death or the differences between the numbers of successive generations in a sample. Furthermore, field experimentation is facilitated by the small size of barnacles, their dense concentrations and intertidal location.

I would like to express my thanks to C. M. Yonge for his advice and encouragement throughout this work. Other members of the Zoology Department of the University of Glasgow provided technical assistance and helpful discussions. My sincere thanks also go to the staff of the Marine Station, Millport, for their help and forbearance, during my stay there. T. B. Bagenal made observations of the study area after I had left and throughout the study provided many stimulating discussions. I would like also to thank Charles Elton and other members of the Bureau of Animal Population, Oxford, for much encouragement and enlightening discussion. E. W. Fager read

the complete manuscript and his suggestions, especially on statistical matters, are gratefully acknowledged. Finally I wish to thank my wife for her constant encouragement and help.

METHODS

The area of study was located on the tip of Farland Point, Isle of Cumbrae, in the Firth of Clyde, Scotland. The shoreline at this point faces south and consists of a series of ledges of Old Red sandstone, dipping downward to the west. These create a series of parallel ravines oriented at right angles to the shoreline. The east wall of each ravine has a slope of about 30° to the horizontal, while the west wall is almost vertical, varying in height from 2 to 6 ft. In the ravines loose pieces of rock varying from a few inches to 3 ft in diameter occurred. Most of the smaller pieces were composed of bostonite, a harder basaltic rock derived from larger dikes in the vicinity.

Detailed studies were made in three areas, located within a 50-ft stretch of this shore (Fig. 1). Area 1 was located on the vertical west wall of a ravine. On this wall, which was about 6 ft high, study plots were located at four levels. At each level small squares, of about 25 cm^2 each and spaced a few inches apart, were marked by drilling shallow pits at the corners. The positions of all the barnacles in each square were mapped. At each level one or more of the squares was covered with a cage of

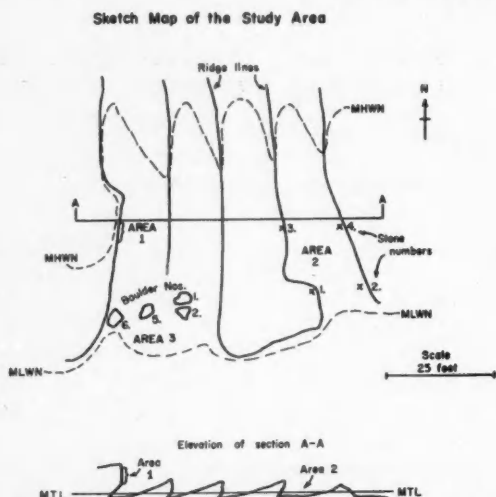


FIG. 1. Sketch map of the study area with approximate contours. Stones 7 and 8 are located on Area 1.

stainless steel wire netting to protect the barnacles from predators.

During the period of this study, moderately strong wave action was observed during gales each year, though probably extreme wave action, such as that on the shores exposed to the open Atlantic, does not

TABLE 1. Descriptions of the areas upon which the periodic censuses of *Balanus balanoides* were carried out.

Area No.	Subdivisions of the area	(Standard tidal levels)	Height in feet, relative to M.T.L.	% of time exposed to air	Descriptions of the small areas at each level where the censuses were made, with the names used for each in the text and figures. The date of first census of each area is given; all were continued until June, 1955.
1.	Top level	(MHWS)	+4.9 +4.2	96 91	Jan. 1953: 3 adjacent squares, mixed <i>Balanus</i> and <i>Chthamalus stellatus</i> ; each 25 cm^2
	High level	(MHWN)	+3.1	79	July 1953: Only censuses of <i>Thais</i> were made at this level
	Upper level		+2.6	75	Nov. 1952: Cage 1, Cover, Control 1: each 29 cm^2 Dec. 1953: Control 2, Cage 3: each 50 cm^2 July 1954: Cage 2: 66 cm^2
	Middle level and stones 7 and 8		+2.1	69	Nov. 1952: Cage 1, Cover, Control 1: each 29 cm^2 April 1953: Stones 7 and 8: 5 to 6 cm^2 Nov. 1953: Control 2, Cages 2, 3, 4: Control, 47 cm^2 , Cages, 92, 98 and 98 cm^2 , respectively
	Lower level		+1.5	63	Nov. 1952: Control 1 and Control 2: 29 and 25 cm^2 respectively Oct. 1953: Cage 1: 61 cm^2 Feb. 1954: Control 3: 52 cm^2
2.	Stones 3 and 4 Stones 1 and 2		+1.1 -0.9	59 42	April 1953: 5 to 6 cm^2 April 1953: 5 to 13 cm^2
3.	Boulder 1		-0.9	42	June 1953: 25 cm^2 in 1953, 47 cm^2 in 1954-5
	Boulder 2		-0.9	42	June 1953: 25 cm^2 in 1953, 53 cm^2 in 1954-5
	Boulder 5		-1.8	35	July 1953: 50 cm^2
	Boulder 6		-1.9	34	July 1953: 50 cm^2
		(MLWN)	-3.0	23	
		(MLWS)	-5.1	4	

NOTE: The areas of census on the stones were different in each settlement season; the sizes are included in the ranges given.

occur in the Clyde sea area. However, the alga *Alaria esculenta* (L.) Breve, an indicator of fairly strong wave exposure (Lewis 1954b), occurs only at this point on the Isle of Cumbrae. *Ascophyllum nodosum* (L.) Le Jol., an alga which does not thrive in wave-beaten areas, occurred only in the upper sheltered parts of the ravines. *Fucus spiralis* (L.) and *Fucus vesiculosus* L. were the dominant large algae on Areas 1 and 2, *Gigartina stellata* (Stockh.) Batt. on Area 3.

In addition to these squares which were mapped *in situ*, two flat stones of bostonite about 4 inches in diameter were fastened at the "middle" level, 2.1 feet above mid tide level; these were numbered 7 and 8 (Table 1). They could be removed and replaced during the low tide interval and were used to follow the pattern of the spring settlement. All the squares and stones in the three lower levels of Area 1 were located in a space of about 1 m².

Area 2 consisted of two pairs of removable stones located in a ravine about 50 ft east of Area 1. One pair was fastened about 1 ft above mid tide level, the other about a foot below, further down the ravine. Although both members of a pair were at the same level, one was fastened to the sloping east side of the ravine so that it faced upward, while the other member was fastened underneath an overhanging ledge on the west side so that it faced downward. In the lower pair, stone 1 faced down, stone 2 up; in the higher pair, stone 3 faced down, stone 4 up. All these stones were similar in size and composition to those attached to Area 1.

Area 3 consisted of four boulders, each about 3 ft in diameter, situated in the lower part of the same large ravine in which Area 1 was located. The relative heights are given in Table 1. Squares were mapped on the sloping tops of these boulders. A few counts and experiments were made on other rocks in the same area; these will be described as necessary.

The three areas spanned almost the entire intertidal distribution of *Balanus balanoides*. Only scattered individuals occurred above the highest level of Area 1, and below the lowest boulder of Area 3.

The stones and cages were fastened to the rock by means of a stainless steel screw inserted in a plastic tube, sold as a screw anchor, which was fitted into a 1" deep hole, 1/4 inch in diameter, drilled into the rock. One such screw with suitable stainless steel and plastic washers was enough to hold a small stone or cage in place. These remained in place for over two years with no losses. The cages were made from stainless steel wire netting, No. 22 gauge wire, eight meshes to the inch; this netting has an open area of 60%. They consisted of a floorless enclosure about 6 x 6 inches, with walls about 1 inch high, so that the roof was well above the barnacles. In two instances, a piece of netting was stretched out from the side of a cage as a roof over an area of barnacles, but with no sides. This was done in an effort to create a physical environment similar to that in the

cage, yet allowing access to predatory whelks; these were termed "covers."

The surface area used to calculate the population densities given in this study was that of the rock surface projected on to a plane surface. The population density of the youngest age group was calculated on the basis of the "available area" for that group; i.e., the area of free rock surface unoccupied by older barnacles.

Initially, the mapping of each square was done on graph paper, a grid of threads of 1 cm² opening being used as a guide on the rock surface. Later a more efficient method using a piece of thin glass (lantern slide cover glass) was developed. The glass was held over the barnacles and their positions were marked directly on it with glass-marking ink. A paper copy was made from this so that notes could be made after each census. For the first six months after settlement, the individual barnacles were not mapped, but successive counts were made on a small portion of each area. Yellow water color paint was used as an aid to avoid duplication in counting; it washed off during the next few high tides.

In the first census, November 1952, every individual was mapped, and the settlement of that year, then six months old, was distinguished from the rest. It was possible to distinguish these from the older year groups by their smaller average size and the appearance of the shell. Above mid tide level, barnacles aged 6 months had quite thin shells and the upper edges of the wall plates or parieties were still uneroded; the surface was fairly smooth and white. The previous year group, then aged 1½ years, had undergone much erosion so that the upper edges of the shell were thick and rounded, no new shell having been added there. (Growth in the compartments of a barnacle, according to Darwin (1854), occurs only along the basal and lateral edges of each wall plate; erosion of the top edge is not replaced.) The surface was darker and often pitted in these older individuals, probably due to boring algae (Parke & Moore 1935).

The differences in appearance were more reliable than size in separating the youngest age group from all the rest, since there was generally some overlap in the size range at this time. This overlap was noted in measurements made from photographs of the plotted squares which had been under observation for two years; two year classes had settled in this period and at the time of the photograph were 6 and 18 months old, respectively. The same sort of overlap in the extremes of size in the 6 and 18 month age groups was evident in some data kindly provided by Mr. H. T. Powell, from the study of growth rate published in Barnes & Powell (1953). An additional check was provided by the fact that the largest 6 months old barnacles were the most different from the 18 month group in general appearance. Besides having smooth thin shells, these fast growing individuals had increased their basal area faster than their opercular opening, resulting in a low barnacle with a proportionally smaller opercular opening.

No reliable way of distinguishing the various year groups of age $1\frac{1}{2}$ years and older was found. Kuznetsov & Matveeva (1949) state that barnacles from the Arctic coast of Russia have definite annual growth rings. Such rings were not obvious at Millport, perhaps because the seasonal variations in climate were not so great as in Russia.

Copies of the original data of this study have been placed in the Bureau of Animal Population, Department of Zoological Field Studies, University of Oxford, Oxford, England.

Abbreviations for the intertidal shore levels used in this paper are as follows:

MHWS: Mean high water of spring tides.
 MHWN: Mean high water of neap tides.
 MTL: Mean or Mid tide level.
 MLWN: Mean low water of neap tides.
 MLWS: Mean low water of spring tides.

The absolute heights and the percentage of the time in which these levels are exposed to the air are given in Table 1.

SETTLEMENT

METHODS

To determine both the rate of attachment and the mortality during the settlement season, the fate of individual cyprids was followed. On each detachable stone, one small area was examined daily and the positions of the newly settled cyprids were mapped. At every other low tide the stones (from Areas 1 and 2; see Table 1) were brought into the laboratory and examined with a dissecting microscope. A glass slide ruled with a grid was placed over a marked area of the stone and all changes, such as new attachments, losses, and metamorphoses were marked on an enlarged map of the area.

The stones were always returned to the shore before the tide rose again and when in the laboratory were kept outside on a window ledge, except during the brief period when they were being examined. Thus the conditions were little different from those during a normal low tide. That this treatment did not markedly increase the mortality can be seen from the records of Stone 3, which was subjected to the same amount of handling as the other stones. This stone evidently was in a protected place on the shore since the cyprid mortality between attachment and metamorphosis during the 1953 and 1954 settlement periods was only 5%. Some of this mortality probably occurred on the shore, so that the amount resulting from the examinations in the laboratory must have been small.

After the position of a cyprid had been plotted it was assigned a grid number and records of its metamorphosis and/or death were kept. The fate of about 8,000 individuals was followed in this manner over three seasons.

There are several possible sources of error in this method: (1) if any cyprids had been clinging tem-

porarily to the surface between tides instead of being permanently attached, their absence at the next examination would have been erroneously recorded as mortality; (2) some cyprids may have attached and been killed between successive examinations without a record having been made; and (3) cyprids, having cemented themselves down, might be detached and then reattach themselves elsewhere. Evidence that temporary clinging occurred only very rarely was obtained during the last two seasons by picking the cyprids off an area of 4 cm² on each stone with a needle. Fewer than 1% were not cemented down, and these were usually recognizable by their position, lying on the side. The loss of cyprids between examinations seems likely to have been small, since many cyprids did not become detached from the rock for several days after their death. A later study of this species at Woods Hole, Massachusetts, showed that if attached cyprids were removed and placed in dishes of seawater, they could metamorphose and become reattached. The possibility of this occurring in the turbulent water of the intertidal area is small, however, since the antennules by which the initial attachment is effected would be encased in a mass of dried cement.

During the first two settlement seasons individuals were followed on all six stones. In 1955 such records were only made on stones 7 and 8; on the other four, daily counts of small areas were made, but the cyprids were not followed individually.

The stones were kept in the same positions on the shore for the three seasons. Some of the individuals of the 1953 year group were still present at the beginning of the 1954 season so that at this time a small area on each stone adjacent to that followed in 1953 was cleared for observation. A third area was cleared in 1955. Thus the 1953 and 1954 year groups were followed without disturbance until June 1955. The disadvantage of this procedure was that the adjacent areas followed each year may have differed slightly in surface contour. Only on stone 1 was the same area used in consecutive years, 1953 and 1954; this was possible since the 1953 year group disappeared completely during its first winter on this stone.

THE PATTERN OF SETTLEMENT

Fig. 2 shows the numbers of attached cyprid larvae and metamorphosed barnacles as they accumulated on each stone in each settlement season studied. In all cases the pattern is similar; an initial period of low and slightly increasing rate of attachment, followed by a period of 5 days or so in which the rate of attachment was high and finally a return to a low rate approaching zero. This sort of pattern might be expected to result if there were individual variations in speed of development of the nauplii in the plankton following a sudden massive liberation of larvae. A few fast-developing larvae would be the first to arrive, followed by the great bulk of those which had developed at the average rate and the

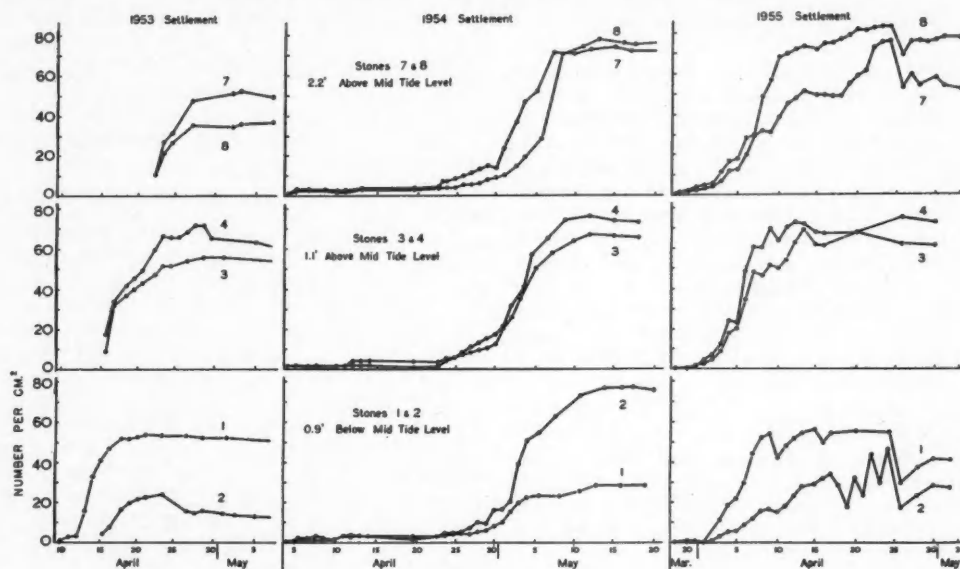


Fig. 2. Settlement pattern of *Balanus balanoides* on the same stones in three seasons at three levels. The density represents all living attached cyprid larvae and metamorphosed barnacles.

attachment rate would decline as the slowest-developing larvae arrived.

Another explanation of the gradual increase in rate of settlement has been suggested by Knight-Jones & Crisp (1953). They pointed out that if previously settled cyprids stimulate others to settle, (as shown by Knight-Jones 1953), the rate of settlement would be proportional to the numbers already attached. No actual data were given although the authors stated that they had repeatedly witnessed such a phenomenon. A decision between the two explanations cannot be made on the basis of information obtained in the present study.

The gradual decrease in settlement rate as the maximum density is approached might also be explained by a gradual diminution in numbers of larvae in the plankton. However, a decrease in settlement rate occurred on stone 1 in 1953 long before the number of planktonic larvae available for settlement had decreased. This is shown in the curves for 1953 in Fig. 2, where the maximum rate of settlement on stones 7 and 8 occurred after April 20, at a time when very few individuals were attaching to stone 1 which had reached its maximum density a week before.

This was investigated during the settlement seasons of 1954 and 1955 by picking the cyprids off small areas of each stone at each examination. In 1954, the settlement on all the stones had reached the maximum by about May 10. After this time the rate on the natural areas dropped to less than one cyprid attaching per cm^2 per tide. On the cleared areas the rates stayed above 4 cyprids/ cm^2 /tide until May 25. In 1955, the same thing was observed on

Stones 7 and 8; the rate on the undisturbed areas approached 0 after May 1, while that on the cleared areas stayed above 3 until May 11. In most instances, the rates of settlement on the cleared areas were much higher than those observed on the undisturbed ones (in 1954, the highest average rates for the 6 stones were: undisturbed, 4.5 cyprids/ cm^2 /tide; cleared, 9.9 cyprids/ cm^2 /tide). This difference may have been due to the presence of body fluids and bits of cement left behind in the process of clearing. These have been shown to stimulate settling (Knight-Jones 1953). The rates from the two types of treatment are not, therefore, comparable. But the fact that the rates of settlement did not decrease appreciably on the cleared areas until long after the rates on the natural areas were approximately 0 indicates that cyprids were available in great numbers in the plankton and that the cessation of settlement shown in the upper parts of the curves in Fig. 2 was not due to an inadequate supply of larvae.

Chipperfield (1948) counted the accumulating settlement of *Balanus balanoides* on pier piles at Liverpool, and also on *Pecten* shells exposed at intervals to study the variations in intensity of settlement. These counts showed that after the settlement had stopped at all levels on the piles it continued on unoccupied shells placed out later. A similar pattern of accumulation of Bacteria and Protista on plates exposed to the sea is given on page 42 of "Marine Fouling and its Prevention," Woods Hole Oceanographic Institution (1952). Other examples of laboratory and natural populations undergoing sigmoid growth are given in Allee *et al.* (1949).

OBSERVATIONS OF THE BEHAVIOR OF ATTACHING
CYPRIDS

The first cyprids attached in the hollows and concave portions of the surface. An analysis of two small portions of Stone 7 in the 1955 settlement season is given in Fig. 3. The settlement began earlier on the concave portion and in the first main period of cyprid abundance it became almost fully occupied. On the convex portion the settlement became dense only during the second increase in the numbers of planktonic cyprids. The cyprids evidently attached to the convexities only after the hollows were filled. This preference of cyprids for grooves and depressions in the surface has been often noted in the literature on barnacles and Crisp & Barnes (1954) have described it in detail.

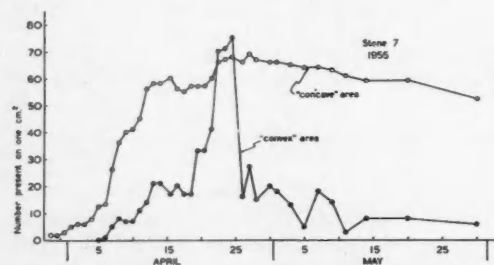


FIG. 3. The settlement of *Balanus balanoides* on two small areas about 5 cm. apart on stone 7 in 1955. The concave area was a hollow adjacent to some adults; the convex one was on a smooth raised area.

Some information was gathered concerning the amount of space needed by a cyprid to effect settlement and the reasons for avoiding densely occupied surfaces. It was noted frequently in the plotted areas that at high population densities the loss of an individual was usually followed by a new attachment on the same spot, usually in the next few days. The searching cyprid may have been attracted by some substance left behind by the damaged individual, or may have detected the open space on the otherwise occupied surface. Underwater, a densely occupied area is covered by a mass of beating cirri which probably would make searching rather difficult.

To test whether cirral activity keeps cyprids from attaching to densely occupied surfaces, the following observations were made. A surface at mid tide level was scraped clean during the 1954 settlement season. At each subsequent examination the cyprids or newly metamorphosed barnacles on one portion of the area were killed with a needle but not removed. The attachment cement held them in place. This created an area of occupied surface having no cirral activity. Another part of the area was kept clear by picking off the cyprids, while on the final part living barnacles were allowed to accumulate. After about two weeks the settlement had stopped on the two occupied areas bearing either living or dead individuals but continued on the cleared area.

It appears that a bare space on a suitable surface, even though it is only the size of a newly metamorphosed barnacle, is the only requirement for a cyprid to attach. Prompt replacement of a missing individual in dense settlements of living barnacles indicates that the surface must be constantly searched, despite cirral activity.

VARIATIONS IN SETTLEMENT

Variation in rate of settlement on closely adjacent areas. To gain information on possible variations in settlement rates in apparently similar situations, the records of the areas cleared on the stones at each examination were analyzed. On each pair of stones at the same level each day's counts were compared separately, as a "matched pair" of values. By doing this, daily variations in the numbers of cyprids in the plankton would not affect the comparison. The data were analyzed by the Wilcoxon matched-pairs test (Siegel 1956). The results are shown in Table 2. Of the six comparisons, significant local variation occurred in three. Variation occurred in both 1954 and 1955 but on different pairs of stones in each year.

TABLE 2. Comparison of the rates of settlement on adjacent areas cleared of cyprids at each examination. Counts were made every 1-3 days in 1954, daily in 1955.

Stone No.	Height from MTL	MAY 1-24, 1954			APRIL 2-MAY 2, 1955		
		No. of observations	Average Set No./cm ² /Tide	Probability	No. of observations	Average Set	Probability
7	+2.1	17	4.3		27	15.8	
8		17	7.1	.001 ***	27	15.5	.316
3	+1.1	15	7.1		28	16.6	
4		15	8.9	.01 **	28	14.6	.102
1	-0.9	14	5.3		28	16.1	
2		14	5.5	.05	28	7.5	.001 ***

NOTE: The data were analyzed using the Wilcoxon matched-pairs test, Siegel (1956).

Since the periods between observations were short, mortality on the shore would probably not account for the observed variation. Nor would it be expected that that patchiness in the distribution of larvae in the plankton would cause such variation between nearby surfaces. The most likely cause of local variability is a difference in surface contour between the two areas. A surface with slightly more irregularity, with more grooves and hollows, would be more attractive to searching cyprids than a smoother surface. It is also possible that such irregularities of the surface may have resulted in the two squares of the pair being of slightly different surface area. Each square measured 2 x 2 cm, but the actual area enclosed was impossible to measure accurately. It was taken as 4 cm² in all cases, so that a difference in surface con-

four of the two stones would cause an error. In the present instance this error is judged to be of much lesser significance than the former reason, in bringing about the observed differences.

Differences in settlement between shore levels. As seen in Table 2, differences occurred in the rates of settlement between shore levels on the stones. An analysis of variance was made of this data, between and within levels, and a significantly greater difference ($p = .05$) was found between the levels. However, the difference in positions of areas 1 and 2 might have created differences other than those due to shore level alone.

On areas of the shore other than the stones, much greater variations in settlement at different levels were observed as follows. On May 3, 1954, when the density of new settlement on the stones had reached about 35/cm² and the adjacent areas were moderately settled, it was noticed that only a very few cyprids were present on the boulders of area 3. (These boulders had been bare of barnacles since winter, as will be described later). The first metamorphosed barnacles appeared on these boulders on May 6, and by May 16 the densities were 16 to 20/cm².

The delayed settlement on these bare areas at a lower level may be explained in several ways. The effect of surface texture must be ruled out, since the boulders were composed of the same type of rock as existed higher up. The most likely explanation for this delay in settlement on large bare surfaces is one based on the work of Knight-Jones (1953). He has shown that larvae of this species and of other sessile marine animals are stimulated to settle by the presence of individuals of their own species. In the situation outlined above, the cyprids attached first to the areas where members of the previous year groups had persisted. Once the space there had become occupied they began to colonize the other surfaces. Barnes & Powell (1953) have suggested that settlement is stimulated by the draining away of thin films of water, such as occurs when the tide rises or falls past a surface; this would occur more often between neap tide limits than above or below. This would not be an alternate explanation for the delay in settlement on Area 3, however, since this area is above MLWN, and so was crossed by the same number of tides as the areas near MTL.

Other authors have observed differences in the density of settlement of *Balanus balanoides* at various shore levels. Fischer-Piette (1932) found the greatest set at low water. Moore (1935b, 1936a) also found the greatest numbers at low water in most localities, but not invariably, a few having the highest density at MTL. Hatton (1938) found that at three locations in two years, the greatest densities were at MTL three times and at LWN three times.

Rice (1935), at Friday Harbor, Washington, counted the settlement density of three species of barnacles. For *Balanus cariosus* (Pallas) the number of adults was greatest at MTL, as was the settlement. *Balanus glandula* Darwin, with no adults present,

settled rather evenly, with slightly more at LWN. *Chthamalus dalli* Pilsbry, with only a few adults present, had equal densities of spat at HWN and MTL and a lower density at LWN.

Thus there does not appear to be any particular level at which the settlement density is maximum. It appears from the study of Rice (1935) that when adults are more abundant at one shore level, settlement is higher there.

Variations in settlement within one season. In 1954, a light set occurred in early April, obviously separate from the main settlement which began in late April (Fig. 2). In 1955, as shown in Fig. 3, two distinct maxima in the rate of settlement on the areas cleared daily occurred in the second and fourth weeks of April, respectively.

Chipperfield (1948) found three maxima in intensity of settlement at Liverpool, spaced 16 and 12 days apart, two at times of spring tides, one at neaps. Pyefinch (1948b), sampling from a pier during the 1947 season at Millport, found that the proportion of total larvae represented by each larval stage varied in a regular manner. Each stage showed three maxima, spaced 15 and 18 days apart. Although his method of collection was not sufficiently quantitative to give accurate estimates of population density, it is probably adequate for estimates of the relative proportions of naupliar stages, especially of the older ones.

These variations probably reflect not the variable behavior of planktonic larvae but successive liberations of nauplii from the parent stock. Crisp & Davies (1955) have shown that the same individual of *Elminius modestus* Darwin may produce several successive broods in one season. The evidence for *Balanus balanoides* is that each individual produces only one brood per year. Pyefinch (1948b) at Millport and Bonsfield (1954) in Eastern Canada examined adults before and after the larvae first appeared in the plankton. They found that only part of the population had released their larvae in the first liberation.

Variation in the sizes of cyprids settling early and late in the settlement season. In 1954, the cyprids which attached in the second week of the settlement season appeared to be much larger than those which had attached in the first week. Measurements of newly metamorphosed individuals, shown in Fig. 4, confirm this. The measurements of the individuals which attached in the first week were actually made during the second week; even so they were much smaller than most of the ones settling that week. The population of small individuals which began to settle in the first week continued into the second, at which time a group of larger barnacles began to arrive; no settlement occurred in the third week, but the size in the fourth week was similar to that in the second. No further measurements were made, but the barnacles which attached in later weeks appeared to be similar in average size to those of the fourth week.

Measurements of attached cyprids and newly metamorphosed barnacles were also made during the other

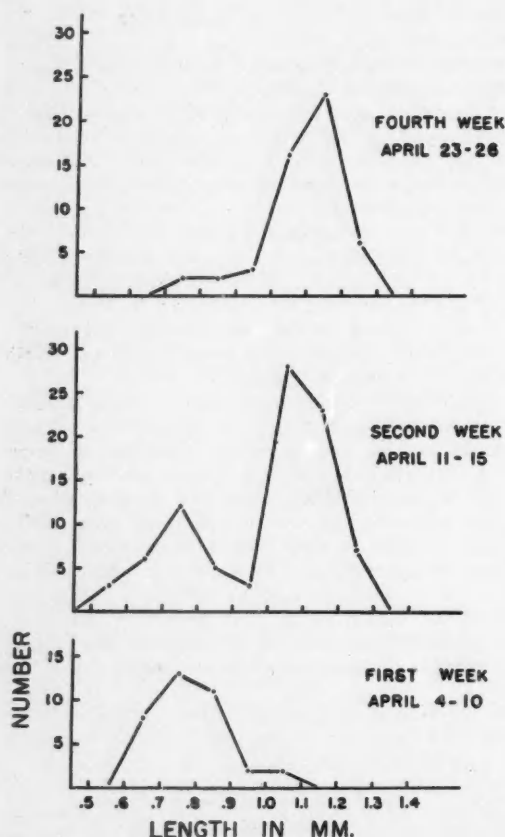


FIG. 4. Frequency distributions of the sizes of newly metamorphosed *Balanus balanoides* which settled during three weeks of the 1954 season.

settlement seasons. These measurements are summarized in Table 3, together with those made by other authors. In 1955 there was no indication of the presence of a distinctly smaller population during the first week such as occurred in 1954. The average size was slightly below that of later settlers, but not significantly so.

The measurements of the other authors appear to indicate a trend to smaller average size toward the southern end of the geographical range. These differences may be misleading, however, since an almost equal amount of variation was found within one season in the present study.

The cyprids which had metamorphosed into the smaller-sized barnacles in the first two weeks were darker and more sharply ridged dorsally than the larger, later, group. The only other species of barnacle which was likely to be settling at this time was *Balanus crenatus* Brug; its cyprids, being much paler (Pyefinch 1948a), did not resemble those discussed above. Cyprids identified as those of *B. crenatus* were found on the stones occasionally, but they never survived.

TABLE 3. Average lengths of cyprids and newly metamorphosed barnacles of *Balanus balanoides* at different periods in the settlement seasons studied. Measurements of other authors are given for comparison.

Present Study, Millport						
Week of Season	ATTACHED CYPRID LARVAE			NEWLY METAMORPHOSED BARNACLES		
	No. Meas.	Av. Length (mm.)	Range of Meas.	No. Meas.	Av. Length (mm.)	Range of Meas.
1953						
4 and 5.....	59	1.0	0.9-1.2	60	1.0	0.7-1.2
1954						
1.....	6	0.85	0.81-0.89	37	0.76	0.64-1.05
2.....	101	1.04	0.72-1.25	98	0.98	0.56-1.21
4.....	75	1.12	0.77-1.25	44	1.08	0.72-1.21
1955						
1.....	29	1.03	0.94-1.14	20	0.96	0.86-1.07
4.....	9	1.11	1.02-1.22	10	1.00	0.76-1.05
Other Authors, Planktonic Cyprids						
Place	Av. Length (mm.)	Range of Meas. (mm.)	Authority			
Herdla, Norway.....	1.20		Runnstrom, 1925			
Altane Fjord, Sweden...		1.02-1.24	Barnes, 1953a			
Millport, Scotland.....		0.84-1.20	Pyefinch, 1948a			
Millport, Scotland.....		0.82-1.22	Barnes, 1953a			
Liverpool, England.....	1.09	0.90-1.25	Chipperfield, 1948			
Plymouth, England.....	0.94		Bassindale, 1936			

During the second week of 1954, measurements were made on each individual cyprid and then on the barnacle into which it metamorphosed. The cyprid measurements were grouped into 1/10 mm classes and the average sizes of the cyprids and the barnacles which had metamorphosed from them were computed. These values are given in Table 4. Cyprids of less than 1.0 mm in length developed into relatively smaller barnacles than did the larger cyprids.

Barnes (1953a) found that measurements of cyprids of *Balanus balanoides* taken from the plankton showed

TABLE 4. The relation of size of cyprid to the size of the barnacle into which it developed. (April 11-15, 1954 only)

Size range of cyprids in each group (mm.)	.70-.79	.80-.89	.90-.99	1.00-1.09	1.10-1.19	1.20-1.29
Number of individuals	1	10	12	37	43	11
Average length of cyprids.....	0.72	0.86	0.98	1.07	1.13	1.22
Average length of the barnacles developing from these cyprids.....	0.86	0.72	0.84	0.99	1.11	1.14
Length ratio, Barnacle/Cyprid.....	0.78	0.84	0.85	0.93	0.97	0.93

two modal sizes. Stage I nauplii removed from adults aged 1 yr collected at a low intertidal level were slightly smaller than those from adults of the same age at a high level. Barnes suggested that the two size groups of cyprids may have come from adults of different shore levels. Although this suggestion remains a possibility, the effects of other factors such as size of parent and conditions during the planktonic stages need to be studied. There is some evidence that planktonic conditions were abnormal in 1954 at Millport. Barnes (1956) found that the phytoplankton bloom which normally develops in early March failed to do so in 1954. The larvae released early into the plankton may not have had sufficient food for proper development, so that the few cyprids which developed from them might have been small.

Annual variations. Records of the occurrence of barnacle larvae in the plankton and on the shore at Millport are available for the years from 1944 to 1955, except for 1948 (Pyefinch 1948b, Barnes 1956, present study).

In every year except 1946, cyprids first appeared in the plankton in early April, although the time of the main settlement varied from early April to early May. In the present study these extremes were encountered in 1955 and 1954, respectively (Fig. 2). Cyprids never settled earlier than March 21, and were never present in large numbers until near the end of March. The subject of annual variation will be treated further following the discussion of mortality during the settlement season.

MORTALITY DURING SETTLEMENT

In most instances it was easy to decide whether an individual barnacle had died in the interval between observations. Missing individuals, those with broken shells and gaping or deeply sunken opercular plates, and cyprids with withered shells, were all recorded as having died since the last observation. In some cases, however, cyprids which never metamorphosed gradually became darker, but remained attached for two weeks or more, so that the exact date of death could not be determined. During the 1955 settlement season, the time between attachment and metamorphosis of 951 cyprids was recorded in daily observations; the average time was 1.5 days. Therefore, the cyprids to which it was impossible to assign a specific date of death were assumed to have died 1.5 days after attachment.

Individuals missing since the previous observation were also assumed to be dead. Detachment in natural conditions is probably accompanied by bodily damage, and reattachment is unlikely to occur, as discussed earlier.

DIFFERENCES IN MORTALITY BETWEEN THE EARLY AND LATE SETTLERS

To study the differences in mortality between groups settling at different periods, the settlement period was divided into weeks and the barnacles which had

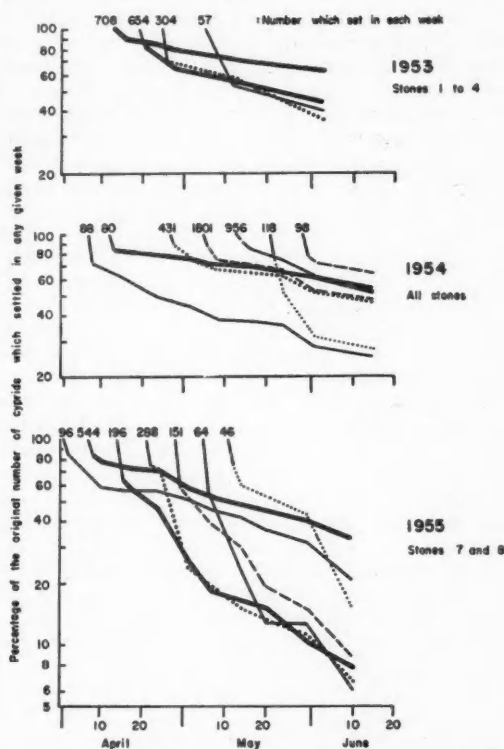


FIG. 5. Survival of *Balanus balanoides* during the settlement season; each curve represents all those which attached during a single week of the season. The first portion of each curve, a thinner line, denotes the mortality of cyprids before metamorphosis. In 1953, the first curve represents the second week of settlement, no records having been kept for the first week. In 1954 there was no set in week 3.

attached in each week were considered as a group. Fig. 5 illustrates the survival of the weekly groups in each year, the barnacles on all the stones being combined. (In 1954 there was no set in week 3).

On each of the weekly survival curves (except the first and last of 1953 when adequate records were not kept), the first segment represents the mortality of cyprid larvae, plotted as if it had occurred in one and half days, as explained previously. Thus the differences in larval mortality are shown by the different slopes or lengths of the first part of each curve. No consistent relationship seems to exist between cyprid mortality and time of attachment. In 1954 the early and late settlers fared worse than the ones during the middle weeks, while in 1955, the reverse was true.

Once metamorphosed, the barnacles which attached in the early weeks appeared to survive better than those attaching in the later weeks. This is particularly clearly shown by the good survival of the barnacles of the second week in all three years; the slope of the curve indicates the relative mortality rate.

The barnacles attaching in the first week in 1954 showed poorer survival. In this year, as discussed previously, the barnacles settling in the first week were of smaller average size than the later settlers.

In 1955 the first cyprids to settle was similar in appearance to the later ones, and their average size was only slightly smaller (Table 3). The survival of the group settling in the first week was poorer during the first two weeks after which it was about the same as that of the second week (Fig. 5). Thus, aside from the obviously different group of the first week, 1954, the survival of the earlier settlers seemed to be consistently better than that of the later ones.

This was especially evident during some of the later periods of heavy mortality, as for example during a gale in the last week of May, 1954. Most of the populations suffered increased mortality at this time, as can be seen in Fig. 5. The percentage mortality for each week on each stone was calculated for this period. These data are shown in Table 5, where percentage mortalities of all the barnacles which attached to the stones in the three early weeks are compared to those of the three later weeks. The percentages for the early weeks were compared to those of the later ones using the Mann-Whitney U Test (Siegel 1956); it indicated that the later settlers suffered significantly greater mortality during the gale ($U = 63$, $p = .025$).

TABLE 5. Mortality during a gale, May 24-26, 1954. A comparison has been made between the mortalities suffered by barnacles which settled early and those which settled later in the settlement season. The figures represent percentage mortality over an interval of three high tides.

Stone No.	EARLY SETTLERS			LATER SETTLERS		
	Weeks No.			Weeks No.		
	1	2	4	5	6	7
1	0	8	22	31	61	78
2	—	—	6	22	28	0
3	0	9	2	1	8	0
4	—	—	19	32	37	—
7	54	14	26	28	39	87
8	—	0	0	3	5	33

NOTE: Only those weekly groups which contained six or more individuals were used.

The barnacles which settled in the eighth week of the 1954 season survived well for the first few weeks, as can be seen in Fig. 5. However, the later survival of the barnacles of this week was poorer than that of any of the other weeks; except on Stone 1, they were all dead within six months. The later survival of those attaching in weeks 1 and 7 was only slightly better. The main bulk of the population present after the end of the settlement season was composed of those settling in the second to sixth weeks.

As discussed earlier, attaching cyprids tended to settle in concavities such as grooves, pits, or other hollows of the surface. Once these places were filled by the early settlers the later ones were forced to settle on the rest of the surface, plane or convex. The differences in mortality on the two types of surface were investigated in the following manner. Two small portions of the area studied on stone 7 in 1955 were chosen, one a concave area where barnacles had persisted, the other a convex one which was almost completely bare at the end of settlement. From the individual records the curves of settlement were constructed and are shown in Fig. 3. The settlement started a week later on the convex area and during the main settlement period in early April only reached one-third the density of the concave area. An increase in planktonic cyprids about April 20, as indicated by increased attachments on an area of stone 7 cleared of cyprids daily, resulted in a rapid colonization of the convex area when the concave areas were almost completely occupied. The gale of April 25th caused great destruction on the convex area, but not on the concave one. The behavior of cyprids which leads them to attach in hollows evidently has great survival value.

This same analysis was used to determine whether the cyprids which attached earlier survived better by virtue of their greater age, when presumably they would have a somewhat thicker shell. The same two areas on stone 7 were divided into the weekly sets and the death rate during the April 25th gale calculated. The percentage mortalities for barnacles which attached during the second, third and fourth weeks are 0, 7 and 8 for those on the concave area and 62, 60 and 92 for those on the convex area. Thus the differences in death rates were much greater between areas than within them. There is some suggestion that within each area the earlier settlers could better withstand the effects of a gale. However the protection offered by the concavity was much more important, indicating that in general the earlier settlers will survive better because they tend to occupy the more protected positions.

MORTALITY AND WEATHER

Since the weather often changed radically from day to day, the 1955 settlement season was chosen for analysis, observations having been made daily in that year. As pointed out earlier, the precise date of death of a cyprid was usually harder to decide than that of a metamorphosed barnacle, so that it would have been difficult to determine any relationship between the mortality of cyprids and daily changes in the weather. Thus for the cyprid mortality, only two periods were analyzed, one being a period of unusually warm, calm weather which persisted for five days, and the other a severe gale. During the warm weather there was no wind, so that there was little lapping of small waves; this prolonged the period of exposure to air. As shown in Table 6, for both these periods the percentage mortality per day of cyprids was much higher than average for the whole season.

TABLE 6. Mortality of cyprids and metamorphosed barnacles during the 1955 settlement season in relation to daily weather conditions.

Daily Weather Type	No. of Days in Each Type	Av. % MORTALITY PER DAY OF BARNACLES		Av. % MORTALITY PER DAY OF CYPRIDS
		Stone 7	Stone 8	Stone 7
Warm, calm.....	5	2.2	0.7	57.0
Warm, light wind.....	3	1.2	0.3	—
Sunny, cold, windy.....	8	4.0	1.7	—
Partly cloudy, cool.....	13	3.6	1.4	—
Rain, over .05 in./day.....	10	2.5	2.1	—
Gales.....	3	16.4	7.1	54.0
Whole season, March 28-May 11.....	42	3.7	1.6	20.0
Number of organisms.....	—	883	452	116

The effect of gales on metamorphosed barnacles was shown in another analysis. The weather occurring in the 1955 season was classified into six types, as listed in Table 6. Then the average percentage mortality per day of metamorphosed barnacles for all the days in each type was calculated. It was unusually great only during the gales. After a gale many barnacles were missing or broken, probably due to debris being thrown about by the waves.

The effect of increased exposure to air at higher shore levels was difficult to ascertain from these data, since the stones were not strictly comparable in surface roughness or angle of attachment. However some comparisons seem justified; the percentage of cyprids which metamorphosed after attachment varied from 95 to 70%. In any one season there was no systematic variation, and the stones at the highest level did not have the highest mortality. The percentage survival from initial attachment of the cyprid to the end of the settlement season varied from 88 to 24%. The highest mortalities occurred on different stones in 1953 and 1954, stones 2 and 4 respectively. Again the stones at the highest level did not suffer the greatest mortality. The erratic nature of these results indicates that chance damage was the main cause of death; stone 3, protected under a small overhang, always had the lowest mortality. Once metamorphosed, the most dangerous time for newly settled barnacles seemed to be when they were immersed.

MORTALITY ASSOCIATED WITH OTHER ANIMALS, INCLUDING INTRASPECIES RELATIONSHIPS.

During the 1955 season, broken barnacles were observed associated with regular grooves, which appeared to be radula marks, on the surface. The most likely cause for these marks was the grazing of the limpet, *Patella vulgata* L., which was very common in the area. An experiment performed during the 1954 settlement season to demonstrate the effect of limpets is illustrated in Fig. 6. At the beginning of barnacle settlement, two cages were attached to a slope of bare rock where radula marks indicated heavy grazing by

limpets. One cage was attached over two limpets, the adjoining cage having none. After the settlement season was over, the photographs in Fig. 6 were taken. It is possible that the restriction by the cages may have resulted in more intense grazing inside the cage than on the open shore. But it seems obvious that the limpets can reduce the density of barnacle settlement appreciably. Inside the cages on Area 1 (described in the next section) the density of settlement in the narrow spaces between the tall older barnacles was very high. This suggests that the limpets present in the cages were not able to graze in these places. Hatton (1938) cleared the limpets away from the area surrounding his settlement sites to prevent the destruction of the young barnacles. He states that the limpets did not damage older barnacles; this was confirmed in the present study by the good survival of older barnacles in cages with limpets on Area 1. Lewis (1954a) noted that the activities of a population of *Patella vulgata* removed the newly settled spat of *Balanus balanoides* above MHWN. Those spat which settled in pits or among older barnacles survived. An indirect effect of *Patella* on *Balanus* has been suggested by Southward (1956). Limpets had been removed from a strip of intertidal shore on the Isle of Man and the recolonization studied (Jones 1948, Burrows & Lodge 1950, Southward 1953). Following the limpet removal, algae colonized the strip, covering it almost completely; after this there was good survival and growth of newly settled limpets under the algal canopy. Their grazing presumably prevented further recruitment of algae so that by the sixth year following the start of the experiment the algae had declined to the original degree of coverage. The density of *Balanus balanoides* (at MTL but not at HWN) declined when the algae increased. Southward (1956) ascribes this to the barrier effect of algae preventing the cyprid larvae from reaching the rock surface. However, several alternate explanations are possible; the increased limpet population may have destroyed more of the settlement than usual. Also, the period of decline in the *Balanus* population coincided with years of poor settlement of this species over much of England, including the Isle of Man (Southward & Crisp 1954). In addition, if more *Thais* occurred under the protective algal canopy this would partly explain why the decrease occurred at MTL where *Thais* was common but not at HWN, where it was never recorded by Southward (1953).

In a visit to Millport in the summer of 1958, similar changes were found; these are summarized in Table 7. *Patella* had decreased, and the cover of larger algae had increased. The algae on Area 1, mainly *Fucus vesiculosus* L., were 10 to 12 cm in length in late June, 1958. Hatton (1938) found that this species grew 20 cm per year at St. Malo, and in Denmark, Lund (1936) found that it grew 9-15 cm per year. Thus the algae on area 1 had probably attached during the summer or autumn of 1957. The 1958 *Balanus* settlement was less dense under the *Fucus* than in the open, possibly due to the barrier

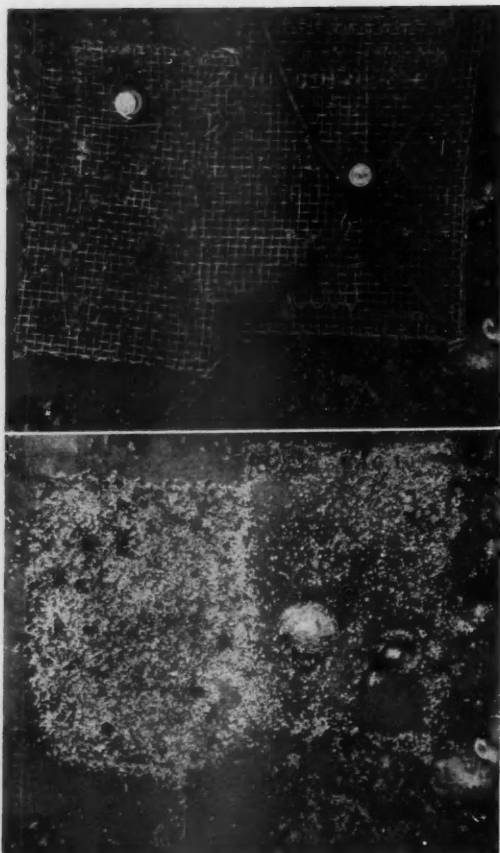


FIG. 6. The effect of grazing by the limpet, *Patella vulgata*, on newly settled *Balanus balanoides*. Both photographs were taken on June 22, 1954, after the cages had been attached for 10 weeks during the settlement season. The left cage excluded limpets, the right enclosed two. Each cage was about 9 x 6 inches in size.

effect of the algae as suggested by Southward (1956), or to the decreased water circulation under algae as suggested by Hatton (1938). The alternative explanations given above would not apply to the 1958 settlement under the *Fucus* since the limpet density was low and, as will be shown later, *Thais lapillus* did not feed much on young barnacles if older ones were available. *Thais* was never observed to feed on newly settled barnacles; possibly very small *Thais* might do so but none were observed at this time.

To investigate the other animals associated with the barnacles, all the organisms on small areas of barnacle-covered rock were collected on several occasions in the summer and autumn of 1953. This material was brought into the laboratory and examined. Collections were made from above and below MTL. The principal groups represented were Turbellarians, Nematodes, Oligochaetes, small Gastropods, Lamellibranchs, Ostracods, and Hydracarina. A few Cope-

TABLE 7. Summer observations on the abundance of *Patella vulgata* and *Fucus*.

<i>Patella vulgata</i> , numbers			
	Area m. ²	July-Aug. 1953	August 1958
1. Area 1.....	1.00	14	5
2. Reef below MTL Large limpets.....	5.80	276	22
Medium limpets.....	5.80	76	8
Small limpets.....	5.80	13	14
3. Area 3			
Boulder 1.....	0.33	20	3
Boulder 2.....	0.30	20	7
Boulder 6.....	0.37	27	11

<i>Fucus spiralis</i> and <i>F. vesiculosus</i> ; % Cover			
		1953-1955	August 1958
Area 1	Upper level.....	5	50
	Middle level.....	5	60
	Lower level.....	10	60

pods, Amphipods, Isopods and insects, *Lipura* (= *Anurida*) *maritima* Guerin and Chironomid larvae, were found, plus a few polychaetes of the species *Eulalia viridis* (O. F. Muller). Only the last species would be likely to be a predator, the others all being very small. Moore & Kitching (1939) observed *Eulalia* opening a barnacle. Several observations of foraging by *Eulalia* were made in the present study; the worms seemed to be searching in all the crevices and empty barnacles. One was seen capturing a large chironomid larva among barnacles, but no sign of any attack on live barnacles was observed. Blower (1957) has reported observations of a centipede, *Scoliopterus maritimus* (Leach) feeding on *Balanus balanoides* at night on the Isle of Man. In the few night visits made during the present study, no centipedes were observed.

To study the larger animals, a fish trap was constructed over an area of barnacles so that any fish or crabs foraging over the surface at high tide would be caught. No bait was used. Six species of fish and three species of crabs were caught during operation of the trap for 19 tides in July and August, 1953. The list of species caught follows:

Fish

Labrus bergylla Ascanius
Ctenolabrus rupestris (L)
Centrolabrus exoletus (L)
Gadus virens L.
Cottus bubalis Euphrasen
Onos mustela (L)

Crabs

Portunus puber (L)
Carcinus maenas (Pennant)
Cancer pagurus L.

Only *Ctenolabrus rupestris* was caught regularly. A few stomachs of each of the above species were examined, and traces of barnacles were found only in

those of *Labrus* and *Portunus*. No blennies, *Blennius pholis* L., which have been found to feed heavily on barnacles, (Qasim 1957) were caught.

The droppings of the Purple Sandpiper, *Calidris maritima* (Brunnich) and the Black-headed gull, *Larus ridibundus* L. were examined but no barnacles were found in them. Rock pipits, *Anthus spinoletta* (Mont.), were common but the observations of Gibb (1956) indicate that *Littorina*, *Idotea*, and dipterous larvae are its principal food. Rats and rabbits were also observed on the shore but no stomach contents were examined.

From this limited survey it would seem that none of these possible predators in their present abundance could cause mortalities among newly attached barnacles comparable with those associated with gales.

From the preceding analysis, the following tentative conclusions may be drawn. The first settlers, by selecting the hollows for settlement, had a better chance of survival than those which arrived after the concavities had been occupied. During severe wave action the convexities on the surface of the rock might be rubbed clean, although older individuals with thicker shells appeared to withstand this. Once metamorphosed, the barnacles suffered little mortality during warm, dry weather as compared to that of the cyprids. Thus most of the early mortality of metamorphosed individuals may have occurred when the barnacles were under water. Limpets were the only animals which appeared to contribute greatly to this early mortality. The average mortality did not increase with height except at levels above MHWN. In 1954 the first group of cyprids was small and dark; their survival was poor. Possibly these were liberated shortly before a failure of the phytoplankton population and so did not develop normally (Barnes 1956).

Some previous work has been concerned with this period of barnacle mortality. Deevey (1947), using the data of Weiss (1948b), suggested that survival was poorer at times of maximum settlement of *Balanus improvisus* Darwin on continually submerged glass plates in Florida. These data were obtained by comparing the final numbers of barnacles surviving on plates exposed for a month with the sum of the numbers of cyprids attaching each day for a month to a plate wiped daily. At certain times, fewer attached over a month to the plate cleaned daily than survived after a month's exposure on the other plate. This suggests that the wiped plate was less attractive to cyprids than the one which had both a bacterial slime and previously settled barnacles, both of which have been shown to increase the numbers attaching (Miller *et al.* 1948, Knight-Jones 1953). In addition, the maximum number on the panel exposed for a month depended not on the area but on the season, since during the summer the barnacles grew faster and covered the panel with about a third of the number that could find room to attach in winter. Thus from this study no accurate relation between mortality and density can be derived.

There seems to be no other evidence that cyprid

mortality is associated with population density. As seen in Fig. 5 there was no correlation between the weekly cyprid mortality and population size. However, the population density may indirectly affect survival since the cyprids which attach when the surface hollows are filled have a smaller chance of surviving.

FACTORS DETERMINING THE POPULATION DENSITY AT THE END OF THE SETTLEMENT SEASON

The density at the end of the settlement season is the difference between the numbers which attached and those which died during the season. In the previous work on barnacle settlement, no measurements of the mortality during the settlement season were made, so that it is difficult to decide which factors determined the densities observed.

In some instances, it was obvious that a low settlement density was the result of a limited supply of larvae from the plankton. Hatton (1938) noted that the density of settlement for *Balanus balanoides* at St. Malo was lower in calm areas than in those with moderate currents or waves. He attributed this to the fact that the numbers of larvae brought to the shore were fewer when the circulation was slower. In places where large algae (*Fucus*) grew densely the settlement density was lower; he removed the *Fucus* in patches and found that the settlement was heavier on the bare rock. His explanation was that the *Fucus* reduced the circulation close to the surface. No data were available on mortality; however, it seems logical that less circulation would result in fewer larvae being brought to the shore area.

Bousfield (1955) found that *Balanus balanoides* colonized only the lower portions of a large estuary in eastern Canada because the planktonic larvae remained near the surface where they would be carried seaward. Another species, *Balanus improvisus* Darwin, whose larvae were found near the bottom, colonized the upper estuary, probably being carried there in the landward current near the bottom. This is a particularly clear demonstration of the control of local shore distribution by events which occurred during the planktonic phase.

Another method of approach to the question of the importance of planktonic supply in determining settlement density is that of comparing annual variations in both planktonic and shore populations. Studies of this nature have been carried out at Millport since 1944 in connection with work on fouling.

Pyefinch (1948b) found great annual variations in the numbers of planktonic cyprids at Millport in four successive years. In April, 1945, the number of cyprids of all species in the plankton was only 1/10 that of 1944. Yet the density of newly settled cyprids in 1945 was 74/cm², similar to the maximum densities shown in Fig. 2 of the present study. Moreover, counts of young barnacles in April showed that the density in 1945 was about 3/4 of that in 1944. These figures suggest that great variations in the planktonic supply were not reflected in similar variations in

densities on the shore. As discussed earlier, Pyefinch's methods of sampling plankton were only roughly quantitative, but probably were sufficiently accurate to reveal differences as great as in the two years cited.

Barnes (1956) studied the planktonic history of *Balanus balanoides* at Millport, and has summarized his own and earlier records for nine years from 1944 to 1954. In four of these years, termed "failure" years, very few late-stage nauplii and cyprids were found one month after the liberation of larvae into the plankton in early March. In the other five "normal" years, moderate to great numbers of later larvae were collected in late March and early April.

In three of the four failure years the phytoplankton bloom of early March disappeared after a short time while in the normal years it persisted through March. This seemed to be the most likely cause for the failure of the early planktonic larval population. Other influences such as egg viability, predation, deleterious water factors, etc., appeared to have no correlation with these larval variations.

As has already been pointed out, all the adults do not liberate their larvae at the same time. Barnes (1956) stated that during a failure year, a later liberation might develop successfully if there was a late diatom increase such as occurred in 1954. Barnes (personal communication) has also pointed out that the proportion of the adult population which liberates larvae in the first outburst of a failure year, will determine whether there are enough left for a second liberation of sufficient size to populate the shore.

Unfortunately, few data are available on the settlement density in these years. For the normal years of 1944, 1945, and 1949, the settlement density was equal to or greater than that found to be maximal in the present study (Pyefinch, 1948b, Barnes & Powell, 1950). For the failure years, no quantitative data were given although Pyefinch stated that the late liberation in 1946 led to a "light settlement."

For the three years of the present study, plankton data were available to Barnes for only one, 1954; it was classified as a failure year. In 1955, very heavy settlement occurred at the beginning of April; although no plankton data are available for 1955, this early settlement gives a strong presumption for classifying it as a normal year. If it were a failure year, the first liberation would have had to occur far in advance of that of any of the previous nine years. Also, the settlement continued into the third week of May, a normal length of season. 1953 also appeared to have been a normal year since cyprids began attaching in the first week of April, with the heavy settlement in the second week.

As shown in Fig. 2, the maximum density reached was similar on some stones in all three years. The average rates of settlement (no/cm²/tide) on the areas cleared daily ranged from 4.3 to 8.9 in 1954 and from 7.5 to 16.6 in 1955. The maximum rates of settlement recorded in daily observations for the six stones ranged from 5.0 to 10.6 in 1954, and from

10.2 to 20.0 in 1955. The average and maximal rates observed in 1954 were thus about half those in 1955. Thus the second liberation in 1954, although producing a less intense settlement, filled the space available (Fig. 2) and as shown by the settlement on areas cleared daily, continued after the space was filled. The success of the second liberation indicates that the habit of this species of liberating its larvae in successive bursts has survival value in an environment of fluctuating food supply.

Densities determined at the end of each settlement season during the present study are given in Table 8. The light settlement in 1958 was undoubtedly limited by the supply of planktonic larvae. Differences between the three earlier years were smaller.

TABLE 8. Annual variations in the densities of *Balanus balanoides* (current year-group only) at the end of settlement at Millport and at St. Malo, France, from Hatton, (1938).

Millport					
Area	Feet from MTL	No./cm. ²			
		1953	1954	1955	1958
Area 1, Top.....	+4.2	34	17	18	0.8
Stones 5-6.....	+2.5	16	14	18	—
Area 1, Upper.....	+2.6	67	42	56	2.0
Area 1, Middle.....	+2.1	47	31	48	1.0
Stones 7-8.....	+2.1	34	52	35	—
Area 1, Low.....	+1.5	24	15	42	0.2
Stones 3-4.....	+1.1	40	38	57	—
Stones 1-2.....	-0.9	34	52	30	—
Area 3.....	-1.4	17	10	25	0.5
Average.....		35	30	37	0.9

St. Malo			
Level	No./cm. ²		
	1930	1931	1932
Ouest II (HWN).....	8.0	5.8	—
Est II (HWN).....	4.0	5.2	—
Cité II (HWN).....	10.0	11.4	—
Ouest between	23.0	20.0	19.5
Est II and.....	12.0	12.5	13.0
Cité III	22.0	19.5	18.5
Ouest III (MTL).....	23.2	20.2	—
Est III (MTL).....	12.1	12.9	—
Cité III (MTL).....	22.1	19.9	—
Ouest IV (LWN).....	15.3	17.5	—
Est IV (LWN).....	15.0	13.1	—
Cité IV (LWN).....	23.8	13.9	—

In four instances the densities were much lower in 1954, in two, higher, and in the other three only slightly lower than in 1953 and 1955. Comparing the final densities on the stone with the maxima shown in Fig. 2, it is obvious that much mortality had occurred. Since most of the mortality during the

settlement season was caused by scouring of the convex portions of the surface, it is evident that differences in the surfaces chosen from year to year could account for much of the annual variation shown in Table 8.

After I had left Millport, Mr. T. B. Bagenal continued to make counts and photographs on the study areas. Some of his observations on Area 3, together with those which I made in a return visit in July, 1958, are summarized in Table 9. The 1956 settlement was heavy, the 1958 one light. Although no counts were made in 1957, the settlement then must have been at least moderately heavy. This is shown by the densities on Area 1 in July, 1958. The mean densities (no./100cm²) of the 1958, 1957 and 1956 year groups were 74, 270 and 2, respectively; thus the 1957 settlement after one year was much greater than that of the 1958 group soon after settlement. A moderate settlement must also have occurred in 1952, judging by the density after a year, as shown in Table 9. Thus in the seven seasons from 1952 to 1958, the settlement was light in only one. In the four earlier years when some settlement data are available, only one, 1946, had a light settlement.

TABLE 9. Observations of the population densities (no./cm²) of *Balanus balanoides* on Boulder 1, from 1952 to 1958.

Year group	Density after the end of the settlement season (in late June or early July)	Density the following year, at age 12-13 months
1952.....	—	1.0
1953.....	19.5	0
1954.....	14.0	2.5
1955.....	24.0	0.5
1956.....	32.0	—
1957.....	—	0.1
1958.....	1.3	—

Hatton (1938) observed the density at the end of the settlement seasons of three years. These are given in Table 8. Little difference in density was found between the years. This is especially interesting, since the settlement season of 1930 started three weeks later than that of 1931, the two seasons being 6 and 9 weeks long, respectively. This suggests a pattern similar to that described by Barnes (1956) at Millport. In neither place were the fluctuations in the length of the settlement season correlated with the settlement density at the end of the season.

From all these studies it appears that while the density observed at the end of the settlement season may occasionally be severely limited by the supply of planktonic larvae at Millport it was usually determined by occurrences on the shore, there being a vast oversupply of larvae. This situation may also apply to other similar areas, but may not apply on open coasts where larvae may be carried away. At Millport, the mortality was greatest on the exposed

convex surfaces so that the population density could be regarded as varying directly with the proportion of "concave" surface, including in this category the spaces between older barnacles.

It is sometimes tacitly assumed that variations in the supply of planktonic larvae will be reflected in similar variations in the population of adults on the bottom. Thorson (1950) has suggested that in the life of sedentary marine invertebrates which possess a long planktonic larval phase, the most "critical" period is the planktonic stage. Many authors have shown that adults during the breeding season and developing larvae often have narrower tolerances to environmental factors than during other periods in their life cycle. As evidence for his hypothesis, Thorson showed that greater annual fluctuations in biomass of dredged material occurred in three species of bivalve molluscs with a long planktonic larval life than in two species which had short free-swimming phases. However, since no study was made of such factors as the spatial distribution, mortality, and growth, which also might affect the estimates of the biomass of these bottom invertebrates, this hypothesis can only be regarded as tentative.

MORTALITY FROM CROWDING

FACTORS DETERMINING CROWDING

When the settlement density was high, as it was in the present study, the barnacles after a short period of growth soon began to touch one another. In the following discussion, crowding will refer to the process in which barnacles grow while in contact with each other. The degree of crowding is thus determined by the rate of growth, population density and average size.

The growth of *Balanus balanoides* has been well documented in Western Europe. The results of these studies of most relevance to crowding are as follows. Growth is more rapid when there is more water movement, such as on wave-beaten points or in tidal currents, (Hatton 1938, Moore 1935b, Chipperfield 1948). These authors all believe that this is the result of more food being brought to the population by the increased circulation.

Moore (1935b) noted that barnacles packed closely in a groove grew more slowly than adjacent isolated individuals. He suggested that the food in the water flowing over the surface is shared among more individuals at a higher population density. This suggestion is supported by the observations of Chipperfield (1948), also at the Isle of Man. On the other hand, Kuznetsov & Matveeva (1949) suggest that growth is faster at higher densities. Collections were made at three locations in east Murman (Arctic Ocean) at densities of 5, 3 and 2/cm², respectively. Age was determined by growth rings on the wall and opercular plates; the maximum ages were 7 years at the two higher densities and 12 years at the lowest. At the same age, barnacles at the higher densities were larger than those growing at low

TABLE 10. Growth of *Balanus balanoides* in its later years at Millport and St. Malo.

	No. of Barnacles Meas.	SECOND YEAR (10-22 mos.)			THIRD YEAR (22-34 mos.)			FOURTH YEAR (34-46 mos.)		
		Ave. Length (mm)	Mean Specific gr. rate per day x 100	Mean Absolute gr. rate per day x 100	Ave. Length (mm)	Specific gr. rate	Absolute gr. rate	Ave. Length (mm)	Specific gr. rate	Absolute gr. rate
<i>Millport</i> —Mid Cage 1+2.1 ft. above MTL										
1952 set.....	9	3.1	.147	.456	4.6	.086	.395	—	—	—
Pre-1952 set.....	4	—	—	—	5.5	.071	.391	6.7	.041	.275
<i>Millport</i> —(Barnes & Powell, 1953)										
Panel 3: +1' above MTL	31	17.0	.088	1.496	—	—	—	—	—	—
Panel 7: -6' below MTL	26	19.5	.078	1.520	—	—	—	—	—	—
<i>St. Malo</i> —(Hatton, 1938)										
Decolle Ouest, Level II, HWN.....	50	4.4	.154	.678	6.0	.025	.150	—	—	—
Decolle Est, Level II, HWN.....	50	4.6	.136	.626	6.2	.039	.241	—	—	—
Decolle Est, Level III, MTL.....	50	4.2	.135	.567	5.3	.015	.079	—	—	—
Cite, Level II, HWN...	50	4.5	.102	.459	5.7	.033	.188	—	—	—
Cite, Level III, MTL...	50	4.1	.080	.328	—	—	—	—	—	—
Cite, Level IV, LWN...	50	3.9	.089	.347	—	—	—	—	—	—

Note: All measurements were made in mid-February, except for those in Barnes & Powell (1953) where measurements were made in January and October, at ages of 9 and 18 months. The Pre-1952 set in the present study may have included some individuals older than three and four years.

density. Whether the larger sizes found at higher densities were the result of the differences in density or in location is difficult to decide.

Moore (1934, 1935a), Hatton (1938) and Barnes & Powell (1953) recorded seasonal variations in growth rate. Growth was fastest in spring and early summer, decreasing later to a very slow rate in winter. Most of the growth occurred during the first and second seasons; after the age of 18 months the growth was very slow.

The only data published on the growth of *Balanus balanoides* which were followed after the second year are those of Hatton (1938). In the present study, some barnacles were followed through their fourth year on Area 1. Photographs had been taken of the Middle Cage 1 in February in three successive years, 1953-1955. A few individuals were in a clear position for measurement in all three photographs. Only those individuals which could be followed through the entire two year period were included. For the 1952 settlement, nine individuals were measured, at the ages of 10, 22 and 34 months; for the pre-1952 settlements, four individuals were measured at the ages of 22, 34 and 46 months (although some of these may have been even older). The mean specific growth rate (increase in length per unit length per day x 100) and the absolute growth rate (increase in length per day x 100) were calculated for each group for each year. Similar rates were calculated from the data of Hatton over the same periods, and from those of Barnes & Powell (1953) for the period between

the ages of 9 and 18 months. These data are given in Table 10.

Although only a few barnacles were measured in this study, the values indicate that growth continues, at a declining rate, during the fourth year; it was greater at Millport at this age than at St. Malo during the third year. One of the barnacles of the pre-1952 group reached a length of 10 mm after at least four years. In comparing the growth rates at different levels in the intertidal zone, these authors were in agreement that the rate is faster lower on the shore during the first year. At the end of the second season Hatton (1938) found that the differences in average size between levels were reduced; the smaller barnacles at higher levels appeared to have grown faster and caught up with those at low levels. Barnes & Powell (1953) found that the mean specific growth rate was slightly greater at high levels during the second season; the absolute growth rate was about the same, however, so that the barnacles on their lowest panel were still larger than those on the highest panel at the end of the second year. Moore (1935b) found that in the second year the larger barnacles occurred at high levels in some localities, low in others. Evidence will be given later that the results of Moore and Hatton may be explained by predation by *Thais lapillus*, which selects the larger barnacles at lower levels. This selection inevitably reduces the average size of the barnacles at these levels.

From all these data it appears that for barnacles of the same size and age, growth is closely associated with

food supply, being fastest in the spring when phytoplankton is most abundant and, during the first year, faster at lower levels on the shore where the time of immersion for feeding is longer. After the first year, the growth rate decreases with size and age, irrespective of location.

Crowding varies directly with population density, when barnacles of the same size and rate of growth are compared. Fig. 7 shows such a comparison of stones 1 and 2, which were located close together at the same shore level. The intense crowding at high population density on Stone 2 is evident.

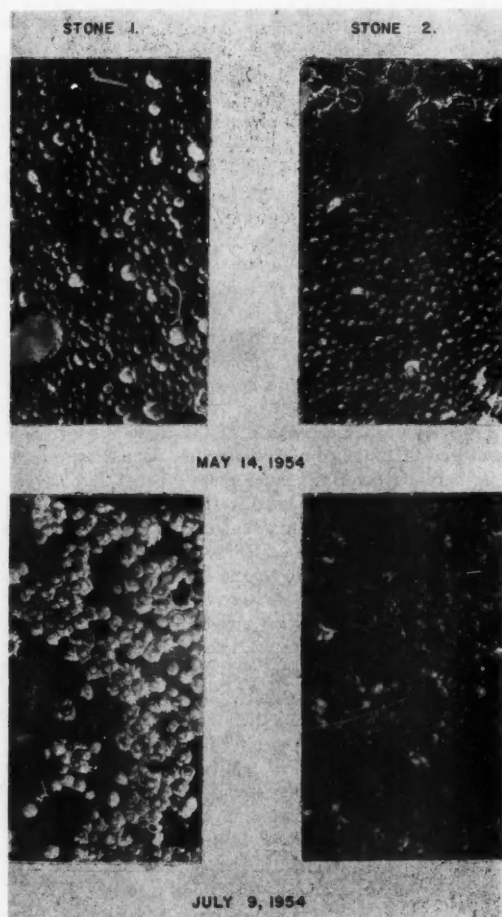


FIG. 7. Photographs of Stones 1 and 2 after most of the settlement of *Balanus balanoides* had occurred and later after some growth had taken place. Each photograph represents an area with dimensions of about 4.5 x 2.5 centimeters.

In populations of the same density, more contacts between barnacles would occur in those composed of large barnacles than in those of smaller ones. However, the increased number of contacts would not necessarily imply greater crowding, since the growth

rate of the larger barnacles might be slower, either because of a lower growth rate, or because of a less favorable location.

PHYSICAL EFFECTS OF CROWDING

Of the many possible consequences of crowding, three will be discussed: (1) changes in growth form, (2) mortality, and (3) impedance of cirral activity. The most obvious results of crowding were the changes in body form of the barnacles. At low levels, or at higher ones where water movement was very rapid, barnacles grew very rapidly; at moderate population densities the barnacles had no room to expand laterally, so grew upward, developing into cylindrical or trumpet shapes. This development was not usually uniform over the surface, local groups developing into "hummocks." The barnacles were attached only at the relatively small base and so were often detached in heavy wave action.

This growth form was ascribed to crowding by Darwin (1854) in England and by Pilsbry (1916) in the United States. Pilsbry states that in *Balanus balanoides* this form "is in no sense a race, as it is commonly found in the same group with patelliform individuals." Darwin (1854), Pilsbry (1916) and Moore (1934) described occasional elongate individuals which were found isolated; no explanation of this was given. This phenomenon has been observed in this species at many other places: in Germany by Trusheim (1932) and Schafer (1948), in France by Hatton (1938), at Millport by Barnes & Powell (1950) and on the arctic coast of Russia by Sokolova (1951). I observed it at Woods Hole, Massachusetts in 1955. It has also been described for many other species by Darwin (1854), Pilsbry (1916), Riee (1935), and Barnes & Powell (1950).

The present observations of the process agree with those of Barnes & Powell (1950). In their study, the settlement densities on the shore were over 80/sq cm, and the barnacles reached a maximum height of 1.3 cm. Hummocking was observed in the present study at densities of 44/sq cm and 16/sq cm; maximum heights at these densities were 2.1 and 1.3 cm, respectively. On Area 3, hummocking occurred only at densities greater than 16/sq cm. Its widespread occurrence, together with the fact that it was observed in each year on the present study area, indicate that it is a common, rather than unusual, phenomenon.

In areas where growth was less rapid, as at the higher shore levels, a variety of body forms resulted from the less extreme crowding. Some individuals retained the normal "patelliform" shape, while others developed cylindrical or low trumpet-shapes and so fitted into the spaces between the "normal" individuals. This elongated condition is shown on stone 2 in Fig. 7, where it is compared with an area of lower density on stone 1 where most of the barnacles were shaped normally.

Besides the effects on growth form, some observations were made on the killing of barnacles by what appeared to be the direct effects of crowding. A series

of photographs taken at short intervals of a dense population of barnacles just after the season of settlement is shown in Fig. 8. During the period shown, 10 of the 24 deaths which occurred were probably a direct result of crowding. Some of these are marked on the photographs; some were flattened laterally (Nos. 1, 2, and 4) while others were undercut and tilted by the growth of their neighbors (Nos. 3 and 6). Once tilted they often dried out, probably because the basal membrane was exposed. A few small individuals situated between larger ones became almost buried by the growth of the neighboring barnacles.

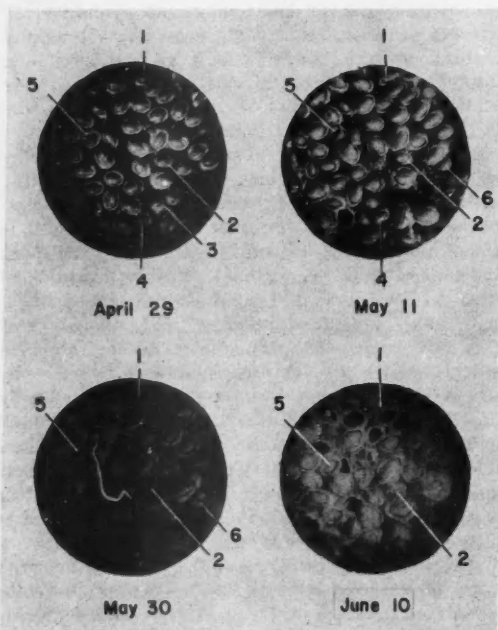


FIG. 8. Photomicrographs of the same area on stone 7 taken at intervals following a dense settlement of *Balanus balanoides*. Some individual barnacles which were being crowded are indicated. Each photograph represents an area of about one square centimeter.

At the higher levels where several year-classes occurred together another effect of crowding was observed. Young barnacles attached themselves to the upper parts of the shells of older ones, and then grew over the opening of the older barnacle, partly occluding it. The older individual usually died, presumably because it was unable to feed. All of these observations were made while following individual barnacles in periodic censuses.

In the present study, the term crowding has been restricted to situations in which crushing, displacement, smothering or distortion of growth form have resulted from the growth of contiguous barnacles. Other authors have used the term in a less restricted sense to refer simply to barnacles existing at a high population density or forming a complete coverage of

the rock. It is probable that these other usages are justified, since certain effects other than those described in this paper may occur in dense populations. One such effect was observed on a stone bearing a dense stand of young barnacles. The stone had been placed in a dish of sea water to observe the feeding movements of the cirri. Three barnacles were situated in a row, the slightly smaller middle one oriented in the opposite direction to the ones on either side so that the direction of beat of its cirri was in the opposite direction to that of its two neighbors. Its beating often coincided with that of one or both of the others, and the continual opposition of its outer cirri with those of its neighbors on either side appeared to inhibit the activity of the middle individual, since its beating was much more irregular and less vigorous than that of either of the other two.

Hatton (1938) in his discussion of the interaction between *Balanus balanoides* individuals, made the following observations. When two young barnacles settled next to each other, one invariably died; the victor was thought to be either the faster grower or the "stronger" of the two. He especially emphasized the effect of the growth of older barnacles in displacing young ones. Only if a young barnacle came into contact with an older one after a sufficient period of growth could it withstand the undercutting of the latter. In the present study, displacement or crushing of a young barnacle by an older one was often observed, especially during the settlement season. However, probably because of the faster growth rate and greater number of the younger barnacles, crowding between them was much more frequently observed than that involving older ones. Hatton also observed a single case of a young barnacle growing over the opercular opening of a three-year-old. The older one died and the younger one survived another year. He also noted that *Balanus* could undercut and remove fronds of the alga *Fucus vesiculosus*. A settlement of *Balanus* removed all the *Fucus* from an area in one growing season. Between individuals of *Chthamalus stellatus* (Poli), he never observed displacement. He suggests that the growth of *Chthamalus* was slower and more continuous than *Balanus* so that the young of *Chthamalus* had time to establish themselves before they could be displaced by the older ones. No observations of the interaction between *Balanus* and *Chthamalus* were given by Hatton. In the present study it was observed that any *Chthamalus* in contact with *Balanus* below MHWN were crushed, smothered, displaced or sometimes lifted on the shell of the *Balanus*. Weiss (1948a) noted in Florida that barnacles on continuously submerged panels were smothered by growths of colonial tunicates and encrusting bryozoa.

MORTALITY ASSOCIATED WITH CROWDING

No method for integrating growth and density into a "crowding index" was devised in the present study. Therefore, to illustrate the effects of crowding on mortality in the following discussion, the ob-

served mortality rate has been considered in relation to variations in growth rate and in population density separately.

At the same population density and average size, faster growth might be expected to lead to more severe crowding, with consequent greater mortality. Seasonal variations in growth would be expected to be reflected in variations in crowding and mortality.

During the first year of life the survival curves often showed a decrease in the relative mortality rate in the winter (Figs. 9, 10, 16, 17), at the time of decrease in the growth rate.

The curves in Figs. 12, 16, 17 and 18 show that barnacles older than two years, if protected from predation by a high shore situation or by experimental means, had a very low mortality rate. The growth of these older barnacles was relatively slow, al-

though they were mingled with younger ones which were still growing rapidly. Evidently the crowding among the younger barnacles had little effect on the older ones, except for the occasional smothering as described earlier.

In Figs. 9 and 10 are shown the survival curves of populations of *Balanus balanoides* at St. Malo, France, from Hatton (1938), as compared to those at Millport. The greater mortality at Millport at MTL, shown in Fig. 10, was probably due to the greater densities of settlement. Near LWN, as shown in Fig. 9, the densities at Millport (Area 3) and at St. Malo were similar, yet the mortality was greater at Millport. Extreme crowding leading to hummock formation had been observed at Millport on boulder 1 in 1953 and on boulder 5a in 1954, followed by complete destruction of the populations. If the

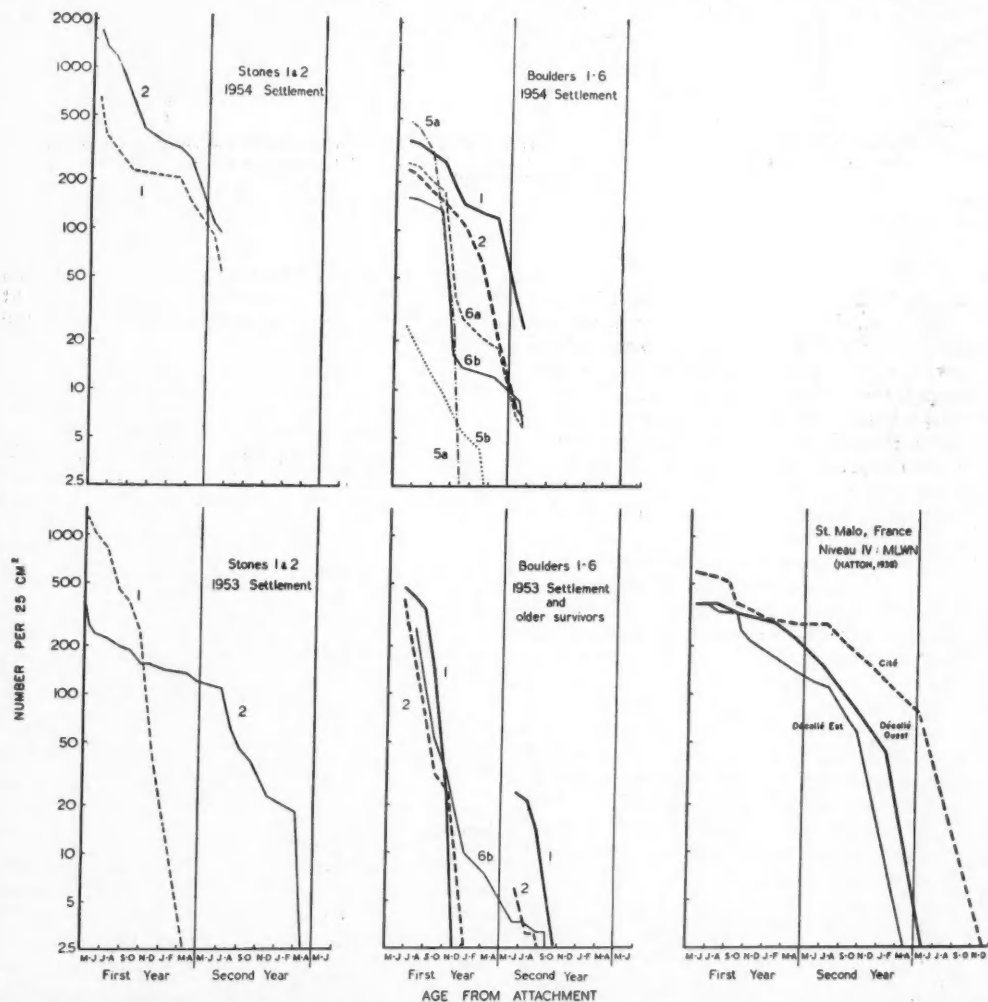


FIG. 9. Survival curves for *Balanus balanoides* below MTL at Millport and in Brittany, the latter re-plotted from Hatton (1938).

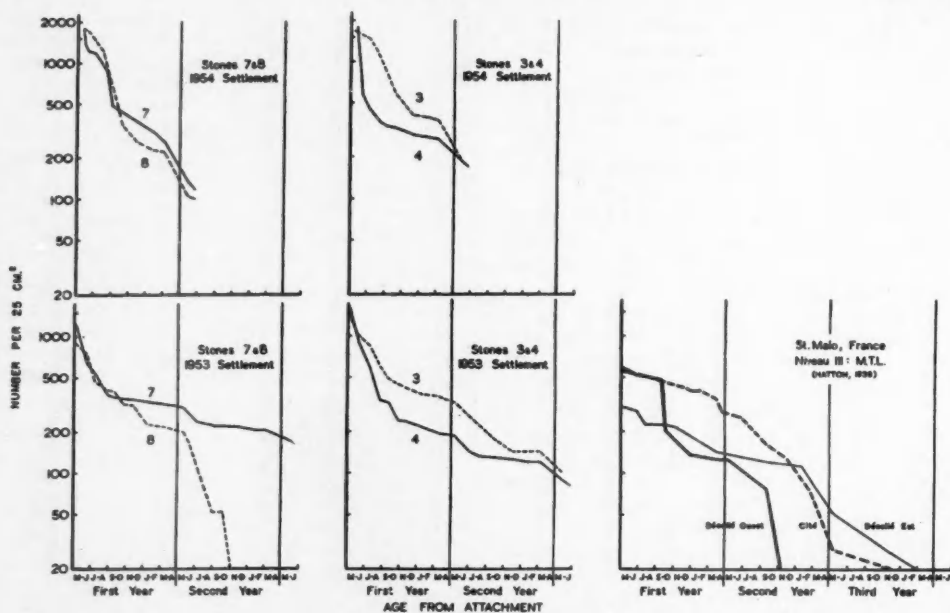


FIG. 10. Survival curves for *Balanus balanoides* just above MTL at Millport and MTL in Brittany, the latter replotted from Hatton (1938).

rate of growth were slower at St. Malo, it would account for the much lower mortalities found by Hatton at similar population densities. Growth rates at Millport during the first growing season were calculated from measurements made of isolated individuals in photographs of the same area near MTL, taken in June and November, 1954. To obtain the growth rate from Hatton's data, the sizes late in August, 1930, were taken from his curves of level III, MTL. This was the date when the maximum size was reached at St. Malo; after this the curves decreased, probably because of selective predation. All the growth rates were calculated as beginning at the same average size as that found in June, 1954, at Millport, 1.9 mm. The time interval from Hatton's curves was taken between the date when the average size was 1.9 mm and the date of maximum size in late August. These readings and the calculated mean specific growth rates are given in Table 11. This method, using only the period of apparent maximum growth at St. Malo while taking a longer span for the Millport measurements, probably tends to underestimate the Millport rates as compared to St. Malo. However, the growth rate was still greater at Millport. At the same population density and shore level, crowding would be expected to be more intense at Millport.

The foregoing analysis has dealt with the mortality during the growing season. However, it must be kept in mind that while some barnacles are killed during the growth period, others may die during the winter as a result of being crowded earlier. This delayed mortality is illustrated by the mass destruction

TABLE 11. Comparison of the growth rate of *Balanus balanoides* at Millport and St. Malo during the first growing season. All barnacles were growing without contact on intertidal rocks.

Millport, just above and below MTL					
JUNE 11, 1954		NOV. 3, 1954		Mean specific growth rate per day x 100	Absolute growth rate per day x 100
Number measured	Ave. length in mm.	Number measured	Ave. length in mm.		
39	1.9	27	4.8	0.59	1.93

St. Malo, data from Hatton (1938). Level III, just below MTL. About 50 individuals in each measurement.

Location	Date when average length was 1.9 mm.	GREATEST AVERAGE SIZE REACHED IN THE FIRST SIX MOS.		Mean specific growth rate per day x 100	Absolute growth rate per day x 100
		Date	Length		
Decolte Ouest.	April 15	Aug. 25	3.4	0.44	1.136
Decolte Est.	May 10	Aug. 25	3.0	0.42	1.027
Cite.	April 18	Aug. 20	3.5	0.48	1.240

in storms in late autumn and winter of populations which had developed the "hummocks" described earlier. Even at levels above MTL, where hummocks rarely formed, crowding produced some individuals of unstable form, squeezed between normally-shaped ones. An analysis of the mortality during the winter on Area 1 is given in Table 12. For those areas at the same level which had higher population densities at the end of settlement, and had thus experienced

TABLE 12. Mortality during the winter months, November through February, in relation to the population density a month after the end of settlement. Only barnacles on Area 1 in cages, protected from predation, were considered. (1954 settlement in their first winter.)

Level of Area 1	Height above MTL in feet	Cage No.	Population Density July 5, 1954	% Mortality Nov., 1954 through Feb., 1955
Upper.....	2.6	1	70	69
Upper.....	2.6	2	27	29
Middle....	2.1	1	57	55
Middle....	2.1	2	23	27
Middle....	2.1	3	24*	27
Middle....	2.1	4	15*	20
Low.....	1.5	1	21	52

* These densities indicate values for July extrapolated back from August 1, when the first counts on these two areas were made.

greater crowding, the mortality during the winter was also higher.

The effect of variations in population density on mortality during the first growing season was investigated by calculating the percentage mortalities for all the squares on Area 1 and for the experimental stones for the six months after the end of the settlement seasons of 1953 and 1954. The relation between these mortalities and the population densities at the end of settlement is shown in Fig. 11. The effect of differences in growth rate is minimized if points representing areas at the same shore level are compared. Except for a few of the areas at the lowest levels, mortality varied directly with density. Above 50 per cm² there was little increase in mortality.

To study the effect of population density on mortality later in life, those populations of Area 1 protected from predation by cages were used. For each year class the percentage mortality was calculated over the same six-month periods as were used in the calculations for Fig. 11. No consistent increase in mortality with increasing density was found in the older groups. Although growth continued in the second season, the densities were low, so that the effects of crowding were reduced within this year group. In the third and fourth summer seasons both the densities and rates of growth were low, as was the mortality.

Another study has been made of the effect of crowding on mortality by Deevey (1947), using the data of Hatton (1938) from St. Malo. He calculated a "crowding coefficient," which was the number of binary contacts per sq cm, a function of population density and average size. When the coefficients were compared to the average expectation of life for the various populations no consistent correlation was found. When the average expectation of life was calculated starting at settlement, populations with from 7 to 76 binary contacts per sq cm showed about the same expectation of life; only the population with a coefficient of about 1.0 had a better expectation.

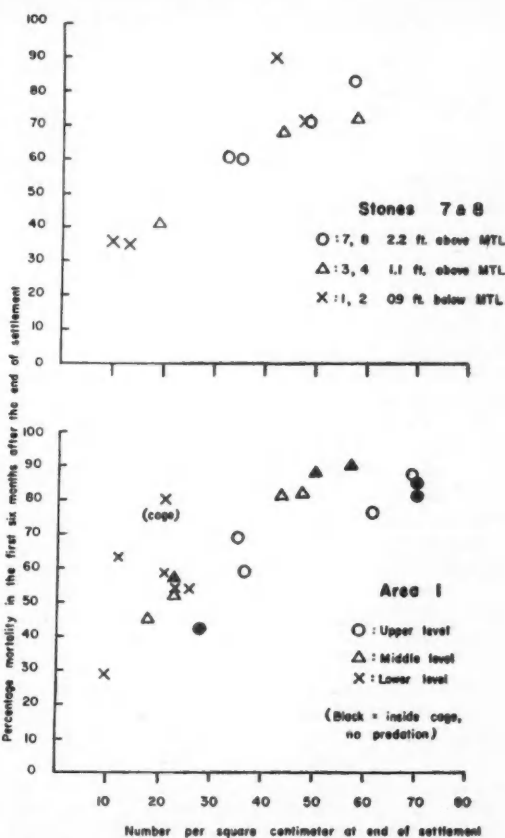


FIG. 11. The effect of population density of *Balanus balanoides* at the end of settlement on mortality during the first growing season. Both the 1953 and 1954 settlements were included.

From the age of 6 months onward, barnacles at high shore levels had high expectation and low coefficients; at other levels there was no consistent trend. These findings agree with those of the present study, that the mortality of older barnacles was not correlated with crowding.

An analysis of Hatton's data was made for comparison with that in Fig. 11. The percentage mortality for the first six months after settlement (May 15-November 15) was not correlated with the density at the end of settlement. This agrees with Deevey's calculation when the first six months were included. The reasons for the differences between these findings and those of the present study shown in Fig. 11 are probably that at St. Malo the densities were low (4 to 24 per cm²) and the growth rate slower, both tending to decrease crowding.

One possible defect in Deevey's "crowding coefficient" is that it ignores the fact that barnacles of similar size may grow at different rates at different shore levels. Thus with the same "crowding co-

efficient," physical crowding might be expected to be more intense at low shore levels; hummocks are seldom encountered above MTL, even though densities may be great.

In an attempt to estimate the proportion of the total mortality which might have been due to crowding, a series of photographs of the area enclosed by the Middle Cage 1 were studied. This area was protected from predation for over 2½ years; photographs taken at intervals during this period are shown in Figure 19. When the area was first mapped in November, 1952, the younger age group, aged 6 to 7 months, was distinguished from the barnacles 18 months of age and older, as described in the introduction.

Of the 62 individuals in the younger group, 48 died within a year; 9 of these were attached to older individuals which died and fell off, carrying the younger ones with them. Eight died in situations in which no crowding was apparent. The remaining 31 deaths, 65% of the mortality, may possibly have resulted from crowding. Some of these occurred in barnacles situated between others which grew appreciably during the year. Where young barnacles were attached high on the side of older ones they often grew rapidly. When this led to their overhanging other young individuals, the lower ones often died, possibly from impedance of their cirral activity or reduction in the amount of water circulating over them; they might even have been crushed by the upper one.

Of the 63 barnacles in the older groups in this cage, 21 died in two years. Nine, or 43%, resulted from crowding. Four were smothered by the growth of young ones attached near the top; five were of small size and may have been crushed by slight growth of their neighbors. Two were carried away when the

shell of a large dead one fell off. Ten died without apparently having been crowded. Some of these were very large and may have died of old age, probably a rare occurrence in natural populations. However, at the upper shore limit of distribution of this species, where predation by *Thais lapillus* is absent, very large barnacles occur commonly. In this situation, deaths from old age may be a regular occurrence; the protection given by the cages on Area 1 seems to have produced a similar situation at a lower level.

When a small population is examined in detail in this manner, it is impossible to assign a definite cause of death in many cases. However, the good correlation of higher mortality with faster growth and higher population density indicates that crowding was one of the important influences in the populations studied at Millport. As growth slowed with increasing size and age, the importance of crowding decreased as that of predation increased.

MORTALITY AT HIGH SHORE LEVELS

THE UPPER LIMIT OF *Balanus balanoides* DISTRIBUTION.

Near HWN the upper limit of distribution of *Balanus balanoides* merged into the bottom of the narrow *Chthamalus stellatus* zone. Little crowding occurred at this level since the population density was low and growth slow. Three squares were mapped above MHWN on the rock face above Area 1. A cage and netting "cover" were attached at first, but since no *Thais* were observed at this level and since the survival was the same after a year on all the squares, the cage and cover were removed. The results of these counts are given in Fig. 12, all three squares being combined. This will be referred to as the Top level, Area 1.

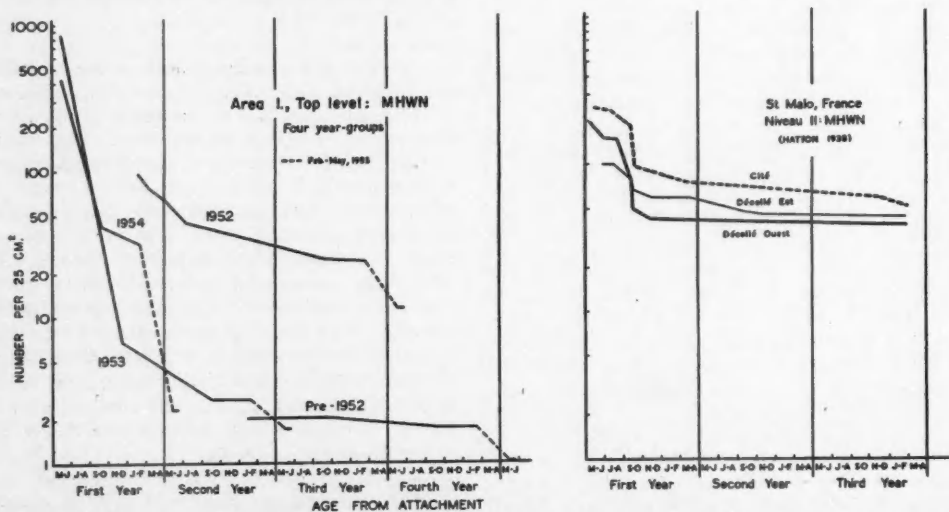


FIG. 12. Survival curves for *Balanus balanoides* at the top level, Area 1, (where it was mixed with *Chthamalus stellatus*); curves from a similar level in Brittany were replotted from Hatton (1938).

In the first mapping in December, 1952, the 1952 year class was distinguished from the previous settlements by its smaller size and the smoother appearance of the shell surface. As explained earlier this method is probably valid for distinguishing the youngest age class from older classes. Because of the slow growth at this level the average size difference between the first and second year individuals was less than that of the populations low on the shore. For the small number of individuals where uncertainty existed, the numbers were divided equally between the 1952 and the older group.

The data from the equivalent level at St. Malo from Hatton's (1938) study are also shown in Fig. 12. At both places the greatest mortality occurred in the first six months after attachment. The survival was good after this except for the spring of 1955 at Millport; this heavy mortality will be discussed later.

The curves in Fig. 12 were arranged so that the survival of the different year classes could be compared at the same age. Only the 1952 year class survived well after the first year of life, and except for a short time after each settlement season, outnumbered the other year classes for the whole study period. The almost complete destruction of the 1953 class soon after settlement eliminated that group; for the 1954 class the early mortality was less but the mortality in 1955 at eleven months of age greatly reduced the density. The 1952 group probably had an unusually favorable period in early life. It and the pre-1952 and 1953 groups were better able to withstand the heavy mortality in the spring of 1955, apparently by virtue of their greater ages.

At this level on the shore, where some individuals survived for at least four years, one year class outnumbered the rest. The occurrence of a "dominant year class" is common in fish populations. Most workers in fisheries biology who have studied this problem have concluded that it had resulted from variations in the survival of the planktonic larvae (cf. Hjort 1926, Sette 1943, Carruthers *et al.* 1951). In the present barnacle populations the recruitment from the plankton was remarkably uniform from year to year. The "dominance" of the 1952 year class shown in Fig. 12 was the result of variations in mortality within the first year after settlement. At lower levels where the length of life was rarely more than two years, there was obviously no opportunity for dominant year classes to exist. Where areas had been protected for a long time from predation, members of the older year classes occupied most of the space (cf. Fig. 19), when normally they would probably have been eliminated by predation.

AN UNUSUAL OCCURRENCE OF HIGH MORTALITY IN THE UPPER SHORE LEVELS.

Sometime between the censuses of mid-March and early June, 1955, great mortality occurred at and above the upper level of Area 1, as shown in Figs. 12 and 16. This mortality might have been expected among the barnacles which were still growing and

crowding each other but its occurrence among older barnacles at the top level and inside the cages at the upper level was very unusual. The mortality rate was much lower during the period before the next census in late June.

Predation was not involved since the caged populations also suffered this mortality; no instances were observed of older barnacles being smothered by younger ones. The mortality during this period of the *Chthamalus stellatus* on the top level of Area 1 is compared to that of *Balanus balanoides* in Table 13. All ages of *Balanus* suffered heavy mortality, while only the youngest *Chthamalus* died in great numbers. A similar but lesser mortality occurred during this period at the middle level but almost none at the lower level of Area 1 (Figs. 17 and 18). This progressive lessening of mortality at lower levels suggested that the cause might be related to some deleterious effect of exposure to air.

TABLE 13. Mortality of *Balanus balanoides* and *Chthamalus stellatus* from February 13 to May 28, 1955 on Area 1, Top level (MHWN).

	AGE GROUP			
	Older than 1952	1952	1953	1954
Number present, Feb.: <i>Balanus</i>	5	70	8	93
<i>Chthamalus</i>	173	42	143	159
% Mortality by May: <i>Balanus</i>	40	53	37	92
<i>Chthamalus</i>	0	0	5	62

A tide gauge had been operating for a year previously at Keppel Pier, 1/2 mile north of the study area. With the aid of the tidal records, an analysis of the degree of exposure to air of the Upper level on Area 1 was made.

Measurements on Area 1 indicated that the height of the upper level was 8.6 ft above Ordinance Datum, and that the vertical amplitude of the waves was 2.5 times that recorded by the tide gauge. The ability of the gauge to record waves was very important, since it was necessary to determine how long the level concerned remained dry. The gauge recorded the waves caused by the frequent steamer passages which would wet levels above high tide even on very calm days. Each such passage resulted in a series of waves lasting less than one minute.

The records from March 1954 to May 1955 were examined and all high tides which did not reach 8.6 ft were noted. The only periods of exposure longer than three high tides during this time occurred in March and April, 1955, when such periods of 4 and 6 tides respectively, occurred. The weather in April was warm and calm, whereas during the period of exposure in March it was cooler and rainy.

The period in April was investigated in detail; between April 16 at 0540 and April 18 at 2110 the level was untouched by any wind-driven continuous

waves. Between these times waves caused by steamers passing close to the shore wet the level only six times, occurring in three of the four high tides.

This exposure of about 60 hours with only six short wettings appears to have been fatal to many of the barnacles. Previous exposures of shorter duration did not cause such high mortality. It would probably be safe to say that no such long exposure had occurred in the past 2 1/2 years, since no similar mortality of older barnacles had occurred on the top or the upper level of Area 1 (Figs. 12 and 16). In this locality the combination of calm warm weather and the very small amplitude of neap tides is evidently fairly rare.

At the top level of Area 1, the effects of these rare periods are probably the main causes of death for those individuals which survive the period immediately after settlement. The survival curves in Fig. 12 indicate that very little mortality normally occurs after the first year of life so that accidents must be very rare; death from old age may occur in a few cases.

Since the unusual mortality of 1955 occurred within and just below the zone of *Chthamalus*, it may have provided space for a downward extension of *Chthamalus* in its autumn settlement. The settlement of *Balanus* in late April filled the existing spaces but the delayed detachment of dead individuals during the summer would probably provide more bare areas than in years when no such mortality occurred.

Hatton (1938) dealt at some length with the settlement, growth and mortality of *Balanus balanoides* at high shore levels. The density at the end of settlement and the growth rate at his level II, HWN, were lower on surfaces which faced south than on those which faced other directions. If shade was provided, the density was the same at all orientations. Since all the surfaces dried out quickly in the shade, Hatton considered that the observed differences were a result of the effects of direct sunlight.

Young barnacles were observed to settle during spring tide periods up to 1 1/2 meters above the adults; the young usually all died during the next period of neap tides. Hatton placed rocks bearing newly attached barnacles above the tidal range; all were dead after a week of continuous exposure to air.

Hatton transplanted rocks bearing barnacles from his level II at HWN to level I at HWS, where no adults occurred. In an observation a week later it was found that the very young barnacles were all dead while those aged two months and any older adults lived four to six months longer. In contrast, young *Chthamalus stellatus* moved from levels II to I suffered only 26-40% mortality after nine days; adult *Chthamalus* occurred normally at level I. Settlement densities and growth rates of *Chthamalus* at these levels were similar on surfaces facing south or north.

Hatton performed two other interesting experiments. He fixed a basin of sea water at HWS with a tiny hole so that the water dripped slowly out. Young

Balanus survived and grew for three months only where the rock was wet, even though the salinity of the water varied. He also transplanted rocks bearing barnacles two years of age from levels IV to II, LWN to HWN. Barnacles of this age left at LWN lived only a few more months, but the ones moved to HWN lived there for two more years, resembling those which had lived at this level all their lives. Southward (1958) found that *Chthamalus stellatus* could withstand higher sea water temperatures than *Balanus balanoides* in the laboratory. Both species endured water temperatures greatly in excess of those which occur in their natural environment. The relative tolerances of the two species confirm the present findings and those of Hatton that *Chthamalus* lives higher on the shore because of its ability to withstand greater extremes of heat or desiccation. These factors, probably in combination, determine the upper limit of *Balanus* distribution, acting more severely on the barnacles in their first year.

PREDATION BY *THAIS LAPILLUS* ON *BALANUS BALANOIDES*

This interaction was studied by determining the seasonal variations in population density, movement and feeding rates of *Thais*, while at the same time recording the mortality of *Balanus* populations either protected from *Thais* by cages or open to predation.

POPULATION DENSITY OF *Thais*

At each visit to the study area, counts were made of the numbers of *Thais* on certain areas, such as the boulders of Area 3. Also, a map of Area 1 was made showing the position of rock irregularities and cages; the positions of the whelks were plotted on copies of this map at each visit. These records were used to calculate the population densities at different levels on Area 1, corresponding to those levels where the barnacles were being studied. In 1953 and 1955 some of the *Thais* were numbered with India ink on a small part of the shell which had been filed clean. When dry, the number was covered with a mixture of "Distrene," a transparent plastic, dissolved in xylol, as described by Quayle (1952).

It was assumed that those whelks which occurred on areas covered with barnacles were actively feeding. By slowly tilting one of these whelks away from the surface, it could usually be observed to be feeding on a barnacle, whose opercular valves would often be gaping open. Of about 400 whelks thus observed on Area 3 in May, 1955, two-thirds were found to be actively feeding. The remaining third were clinging to the rock or to a barnacle, but not feeding; it is probable that these whelks were exposed by the tide while moving from one barnacle to the other. In crevices, on the under sides of boulders, or among algae, whelks were observed which were not feeding.

The average density of *Thais* at various levels on Area 1 is given in Table 14; each level was divided into seaward and landward halves. No *Thais* were

TABLE 14. Distribution of *Thais lapillus* on Area 1, at different levels and seasons. For the "coefficient of dispersion" values, 1.0 indicates random occurrence; those in brackets did not deviate significantly from random. All the others show aggregation.

Side and Level	AVERAGE NO. PRESENT PER OBSERVATION ON 0.1 m ²				FISHER'S "COEFFICIENT OF DISPERSION" ON EACH AREA OVER THE STATED PERIOD		
	All seasons	Autumn	Winter	Spring	Autumn	Winter	Spring
		1953 & 1954	1954 & 1955	1954 & 1955	1953 & 1954	1954 & 1955	1954 & 1955
<i>Seaward Side</i>							
High level.....	1.9	4.2	0.3	0.7	2.7	(1.5)	(1.3)
Upper level.....	4.7	7.8	0.8	2.7	10.5	(1.5)	2.9
Middle level.....	4.8	7.5	1.0	4.4	6.4	(1.4)	2.4
Lower level.....	8.3	12.5	3.7	6.2	4.7	2.4	2.9
<i>Landward Side</i>							
High level.....	0.8	0.7	0.6	0.4	1.6	(0.9)	(1.2)
Upper level.....	3.8	4.8	0.6	2.2	(1.4)	2.0	4.6
Middle level.....	3.4	3.0	0.9	3.7	3.5	2.0	3.0
Lower level.....	3.2	6.5	1.7	2.7	3.2	3.4	(1.3)
No. of observations in each season.....	141	34	46	61	34	46	61

ever seen at the "top" level of Area 1. The whelks were more abundant on the seaward side at each level. The density at the highest level was markedly less than that lower down, but there was little difference between the other levels, except that the seaward side of the lowest level supported a much higher density than the others. It seems that the inhibiting effect of increased air exposure began to be important only at the high level of Area 1, just below MHWN.

In Table 15 the population densities of *Thais* are compared between the low level of Area 1 and three of the boulders of Area 3. The monthly means were used, since the number of observations in each month varied; the period between January and June, 1954 was excluded from the calculations since Area 3 was bare of barnacles at that time, while Area 1 had barnacles. Boulder 6 had significantly fewer *Thais* than the other two boulders, but no other differences of this magnitude were found. The *Thais* population on boulder 6 showed the greatest fluctuations (Fig. 13) and the lowest density. As shown in Fig. 9, this boulder also had the fewest barnacles.

TABLE 15. Population densities of *Thais lapillus*, Areas 1 and 3. The values are averages of the monthly means (see Fig. 13 and 14), excluding the months of January to June, 1954.

Area	Ht., feet above or below MTL	No. of monthly means used	Mean no./m ²
Area 1, Low level only.	+1.5	14	54.5
Area 3, Boulder 1.....	-0.9	14	76.5
Area 3, Boulder 2.....	-0.9	14	88.5
Area 3, Boulder 6.....	-1.9	13	56.1

Using the Mann-Whitney U test, the monthly means were compared between pairs of each of the four areas. The only significant differences ($p=0.05$) found were those between boulders 1 and 6 and between boulders 2 and 6.

Several other authors have made observations on the distribution and abundance of *Thais*. Moore (1938b) on the island of Skye, counted the maximum number, 200/m², at a level between MTL and HWN; the density decreased above and below. *Thais* did not extend upward as high as did *Balanus*; whelks of less than 0.5 cm height occurred only below MTL. Barnes & Powell (1950) counted the whelks during the summer of 1949 at Millport at three levels, MTL, LWN and below LWN. More *Thais*, to a maximum number of 150/m², occurred at MTL than at the lower two levels. The lowest area never had more than 12/m². As the barnacles were stripped off by wave action in the autumn, the numbers of *Thais* also decreased to densities of 3-25/m² in November. Southward (1953), at two localities between the neap tide levels on the Isle of Man, gave average densities of 1.0 and 0.5 per m², with maxima of 31 and 12 per m². These *Thais* were all feeding on barnacles. From all these observations, it appears that on shores covered with barnacles, *Thais* is most abundant at mid shore levels. The upper limit is probably a result of decreased tolerance to increased exposure to air, while the decrease toward the lower levels may be a reflection of the decrease in the population density of barnacles, as on Boulder 6, Area 3.

Whelks were sometimes observed in dense groups rather than scattered over the area at any one level. This was sometimes due to the presence of a concentration of their prey, as when on two occasions cages temporarily were removed (Fig. 16), so exposing barnacles which had been protected for some time. In both cases, these barnacles were much larger than those on the surrounding area; since *Thais* selects larger barnacles if given a choice, this was obviously an area on which they might be expected to feed. In both instances, the whelks congregated on the

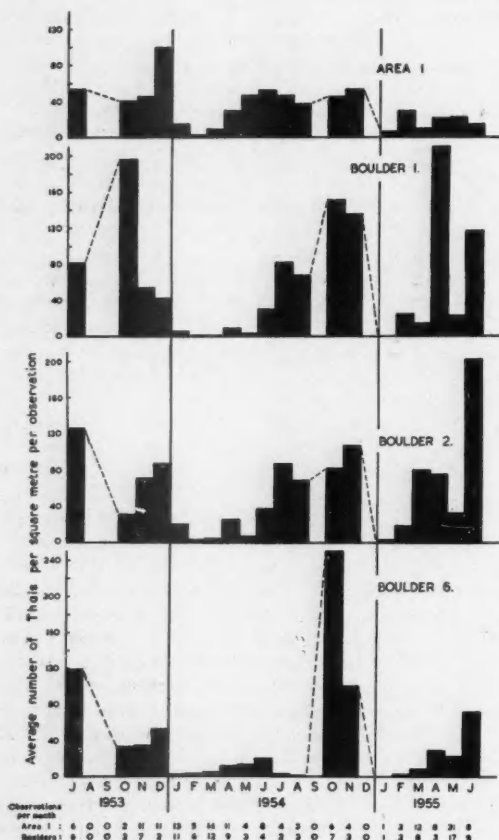


FIG. 13. Average densities of *Thais lapillus* for each month on Areas 1 and 3. When no observations were made during a month a dashed line crosses the space.

small area where the large barnacles occurred so as to almost completely cover it.

During any one season the numbers of whelks which were observed to be feeding on the barnacles varied greatly from day to day. This irregularity in occurrence was analyzed by the same method used to study spatial distribution. Fisher's "coefficient of dispersion" (Blackman 1942, Holme 1949), calculated by dividing the variance by the mean, was used. The formula used was:

$$\frac{\sum (x - \bar{x})^2}{\bar{x}(n-1)}$$

The limits of significance were calculated using the formula:

$$1 \pm 2 \sqrt{\frac{2n}{(n-1)^2}}$$

The results of this analysis are given in Table 14. A coefficient of 1.0 indicates a random distribution; all the coefficients which were significantly different

from a random distribution were greater than 1.0, indicating aggregation.

This variation is probably a result of short term changes in weather; during gales or periods of cold weather, whelks tended to congregate in crevices, on the lee side of boulders, or in algal growths. This variation in occurrence would tend to make estimates of density less precise than if the whelks occurred regularly or at random.

In Figs. 13 and 14 are shown the monthly mean population densities of *Thais* on Areas 1 and 3. The lowest densities were found from January to March, during which period the temperature of the

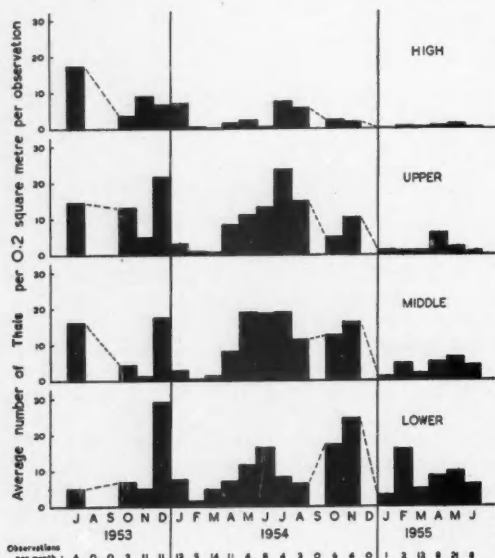


FIG. 14. Average densities of *Thais lapillus* for each month on each level of Area 1. When no observations were made during a month a dashed line crosses the space.

water was at its minimum (Barnes, 1955). An exception to this occurred in February, 1955 at the lower levels of Area 1.

The few individuals which were observed feeding in winter were mostly small, with thin lips to the orifice of their shells. The higher proportion of young individuals among those feeding in the winter is shown by several counts made at different seasons, when large and small whelks were distinguished (Table 16). Moore (1936b) has shown that this thin-lipped type of shell indicates immaturity. Moore (1938a) showed that the tissue weight of mature *Thais* dropped sharply in February and March, and then began to increase. Immature whelks showed no such drop in weight in winter. Moore ascribed the weight decrease either to loss of reproductive products or cessation of feeding by mature whelks during the main spawning period, January to April.

TABLE 16. Proportion of immature *Thais lapillus* in the population in the different seasons.

Month	No. of observations	Total No. <i>Thais</i> observed	No. of <i>Thais</i> which were small, lips of orifice thin	% of total which were small
Area 2, MTL				
December, 1953.....	5	151	85	56
January, 1954.....	10	147	105	71
February, 1954.....	3	45	39	87
March, 1954.....	5	19	14	74
April, 1954 & 1955.....	4	24	7	29
Shore transect, HWN to LWN, most <i>Thais</i> found at MTL				
August, 1953.....	1	1344	576	43
Area 1, above MTL				
February, 1955.....	1	43	40	93
March, 1955.....	1	12	7	58

From the present evidence, it seems that the latter reason may account for much of the decrease.

The seasonal variation in numbers of *Thais* observed feeding at any one location may have been a result both of changes in the proportion of time spent feeding and of changes in the total population size. If it is assumed that in the same month in two different years *Thais* spent the same proportion of time feeding, a comparison of the numbers observed in the two months should reveal any annual changes in population size. In the records of *Thais* over two years those in the months of August, September, December and January were inadequate. For the other eight months an average density was available for each month in two successive years (Figs. 13 and 14).

On Area 1, as shown in Fig. 14, in many of the months of 1954 greater numbers of *Thais* were observed than in the corresponding months in 1953 and 1955. On Area 3 (Fig. 13), the opposite was the case except for the autumn season. Using the sign test (Siegel 1956), the monthly means of *Thais* density in 1954 were compared with those of 1953 and 1955. For Area 1 there were significantly greater numbers in 1954 ($p=.032$), whereas for Area 3 the numbers were significantly fewer ($p=.013$).

For the first months of 1954, Area 3 and the low shore in general was almost completely bare of barnacles, those of the previous year's settlement having been stripped off following "hummock" formation as shown in Fig. 9. With little food at the lower levels it might have been expected that the *Thais* population would shift upward to shore levels at which barnacles persisted, increasing the density of *Thais* at and above M.T.L. That such a shift probably occurred is shown by the low numbers on Area 3 and the high numbers on Area 1.

Thais were first seen feeding on the barnacles of the 1954 settlement on Area 3 in July, 1954. These

barnacles, having settled less densely than those of the previous year, then survived for over a year. Presumably as a result of the reestablishment of this food supply at low shore levels, the density of *Thais* was greater on Area 3 from the autumn of 1954 through June, 1955 than in these months the previous year. On Area 1, changes in the opposite direction were occurring; in the autumn of 1954 the density decreased at the upper levels and increased at the lower levels. The density in the spring of 1955 was much lower at all levels of Area 1 than it had been in the spring of 1954. From these considerations it appears that the annual changes in the *Thais* population shown in Figs. 13 and 14 can be accounted for in large part by vertical redistribution of the population rather than by increases or decreases in the total population size.

There is little published information on mortality of *Thais lapillus*. Orton & Lewis (1931) reported a great mortality of *Thais lapillus* on oyster beds in southern England in an unusually cold winter. In a fecal pellet of the purple sandpiper, *Calidris maritima* (Brunnich), collected at Millport in January, were found 28 spires of small *Thais*. They corresponded in size to whelks 1.9 mm in length. Shells of *Thais* were found in a nest of the herring gull, *Larus argentatus* Pontopp., and oyster-catchers and thrushes have been seen eating *Thais* (Moore 1938b). A few *Thais* were found in the stomachs of two fish, one *Labrus bergylta* and one *Gadus virens*, caught in the intertidal fish trap at Millport in August, 1953. Moore (1938b) estimated that *Thais* may live at least four years on the Isle of Man. In the present study a marked *Thais* lived to an age of at least three years.

None of these observations help in judging whether the mortality rate of *Thais* is greater at any particular season at Millport. Predation by fish would be expected to decrease in winter, while that of birds might be relatively constant throughout the year. Gales occur at all seasons.

As shown in Table 16, the proportion of large older *Thais* was least in February, increasing in the spring as the numbers feeding also increased. This difference in both age structure and numbers was the most pronounced seasonal change in the *Thais* population during the year. One explanation might be that a great number of the large mature *Thais* died in January and that the younger ones grew through the winter so that they appeared in the spring as the mature members of the population. This would mean that few of the *Thais* lived more than a year after reaching maturity and that growth was rapid in winter and spring. Moore (1938a) found that on the Isle of Man *Thais* grew for about three years before attaining maturity, after which time growth stopped. Growth occurred at all seasons at an average annual rate of about 10 to 15 mm, but was somewhat faster in the warmer seasons. In a small collection of *Thais* made in July at Millport, the thin-lipped immature forms had a height range of 1.1 to 2.7 cm, while the thick-lipped mature forms showed a range of 2.5 to

3.4 cm. If the growth rates were similar to those on the Isle of Man, the *Thais* at Millport would become mature in about two years.

The appearance of many large mature *Thais*, often with heavily eroded shells, in the spring makes it seem unlikely that these all developed from the small whelks which constituted the winter feeding population. A more likely cause for the decrease of numbers observed in winter and the increase in spring is that *Thais* spent a smaller proportion of its time feeding in winter and increased the proportion in spring. This would account for the reduction in tissue weight of mature individuals in winter, as reported by Moore (1938a). For each season the density of the *Thais* population is correlated with the sea water temperature (Table 21); this might be expected if the differences in density were a result of changes in activity.

Thais were first counted when they were about one centimeter in height. It takes about 16 months after egg laying for the whelks to reach this size, four months being spent in development in the capsule. Since the main egg-laying season lasts for six months, with some laying all year, and since some individual variation probably occurs, some individuals are probably attaining the size of one centimeter at all seasons. There does not appear to be any particular season when young whelks enter the population in great numbers. Regarding the mortality of *Thais*, the evidence is sparse; no exceptionally cold periods occurred during the winters of 1954 and 1955, and predation did not appear to be

heavier at any particular season. Thus the size of the *Thais* population seemed to be relatively steady, annual variations slight and the seasonal variations probably due mainly to the whelks spending less time feeding in colder periods.

MOVEMENTS DURING FEEDING

Since the positions of the marked *Thais* had been plotted on maps at each observation, movements could be measured. Only those observations made at consecutive low tide periods were used so that each record represents a movement during a single high tide period.

These records do not accurately represent the activity of *Thais* for several reasons. The whelks may not have moved in a straight line, as the distances were measured. In addition, all movements to and from shelter were excluded; these were probably longer journeys than those made while feeding. Thirdly, since the observations were made on a small area, usually about one square meter, the more sedentary individuals would tend to be recorded more often, while the more active ones, once they had left the area, would be missed.

The pattern was usually one of a series of short movements followed by one or more longer movements. For example, three whelks which had been observed for 8 or 9 consecutive low tides showed the following sequence of movements (distances in centimeters): No. 1: 2, 3, 20, 8, 34, 7, 5; No. 2: 2, 14, 11, 31, 6, 28, 17; No. 3: 2, 4, 8, 22, 1, 1, 8, 13. It

TABLE 17. Distances moved by *Thais lapillus* while feeding on *Balanus balanoides*, expressed as a frequency distribution. *Thais* were marked individually and observed at a series of low tides during the periods shown.

Dates:.....	NUMBER OF MOVEMENTS IN EACH DISTANCE CLASS						
	Low shore levels				Area 1		
	July 18-19 1953		July 28-Aug. 2 1953		July 27-30 1953	Dec. 7-16 1953	Apr. 25-May 28 1955
Area:.....	B	C	B	C			
Height from MTL:.....	-0.5	-0.9	-0.5	-0.9	+1.5 to +2.5		
No. of <i>Thais</i> observed:.....	16	28	12	29	4	9	7
No. of successive low tide observations:.....	3	2	12	9	7	7	16
Centimeters moved in one high tide.	0-4.....	20	6	13	65	13	3
	5-9.....	4	8	24	25	1	4
	10-14.....	6	2	18	7	2	8
	15-19.....	3	4	5	4	2	4
	20-24.....	2	8	5	6	0	1
	25-29.....	1	3	1	2	0	2
	30-34.....	0	3	1	3	1	2
	35+.....	7	10	1	2	0	5
	Total no. of observations.....	43	44	69	125	19	24
	Mean distance in centimeters moved per tide.....	14	19	7	8	5	6
							18

is probable that the whelks did most of their feeding during the more sedentary periods.

Most of the observations were made during the summer of 1953. A few others were made on Area 1 in other seasons. In Table 17, frequency distributions of the movements are given. At low shore levels on slightly sloping rocks (series B and C, Table 17) the distances moved during the first, shorter, summer period were much greater than those during the second longer one. This is probably because the more active marked animals, present at first, gradually left the area, leaving only the more sedentary ones to be recorded later. In the second period it was noticed that during some high tides most of the whelks had moved very little, while in others, a greater proportion of longer movements had been made. No correlation of these differences with weather was apparent.

On Area 1, a vertical surface at a higher level, fewer *Thais* were marked. The movements were shorter than at low levels. In December the movements were about the same as in July, but in the late spring of 1955 they were much longer. This difference is probably not due to selection for active individuals, as occurred in the low shore observations, since the period of observation was a long one. Evidently *Thais* is more active in the spring.

THE RATE OF FEEDING OF *Thais* ON BARNACLES

In any predator-prey study, the measurement of the feeding rate of the predator is obviously important. In order to do this, whelks were enclosed in cages with barnacles which were counted periodically. An adjacent empty cage served as a control. The physical

conditions were similar in the experimental and control cages. In the later experiments several cages with *Thais* enclosed were used to provide replicates. Details of the experiments are as follows.

Experiment 1—July 22 to August 8, 1953, at MTL. Two cages were used, one with a *Thais* inside, the other empty as a control. The barnacles were very dense, much crowding occurred, and so many deaths occurred in both cages that the experiment was ended.

Experiment 2—September 10 to December 11, 1953, one foot below MTL. Here the barnacles were scattered and complete counts of living barnacles were made at each examination. Two cages were used, one with a single large *Thais* in it, until October 21; after this two more cages were attached with a *Thais* in each. In December many very small *Thais* began entering the cages so the experiment was ended.

Experiment 3—November 11, 1953 to August 8, 1954. Four cages were attached at the Middle level of Area 1, about one foot north of Cage 1. Two had one whelk each, two were kept as controls. These cages had a mesh of 1/4 inch, but the absence of small whelks above MTL rendered this large mesh satisfactory. In all the other experiments the 1/8 inch mesh was used.

Experiment 4—October 22, 1954 to May 31, 1955. Five cages were attached to a slightly sloping rock surface five yards east of Area 1 at the height of the "Lower" level of Area 1. In three cages two *Thais* were placed in each, in one cage four *Thais*, and one cage was kept as a control. All the whelks had thin lips to the orifice, indicating immaturity (Moore 1936b). One cage with two *Thais* contained

TABLE 18. Feeding rates of *Thais lapillus* (no. of *Balanus balanoides* eaten per day by one *Thais*). The size of *Thais* is the height in cm. See text for method of computing the relative volume eaten.

	Autumn	Winter	Spring	Summer
Experiment 1.				July 22-Aug. 8, '53
Thais size.....				2.0
Feeding rate, number.....				2.0
Feeding rate, rel. vol.....				2.0
Experiment 2.	Oct. 21-Dec. 11, '53			
Thais size.....	2.1 2.8 3.1 Ave.			
Feeding rate, number.....	1.9 2.4 0.7 1.7			
Feeding rate, rel. vol.....	3.3 4.1 1.2 2.9			
Experiment 3.	Nov. 11, '53-Jan. 26, '54	Jan. 27-Mar. 14, '54	Mar. 14-Aug. 8, '54	
Thais size.....	2.0 2.5 Ave.	2.0 2.5 Ave.		2.0
Feeding rate, number.....	1.4 0.5 0.9	0.1 0.01 0.05		1.4
Feeding rate, rel. vol.....	1.9 0.9 1.4	0.2 0.03 0.12		2.5
Experiment 4.	Oct. 23, '54-Jan. 6, '55	Jan. 7-Mar. 25, '55	Mar. 26-May 31, '55	
Cage no.....	1. 2. 3. 4.	1. 2. 3. 4.	1. 2. 3. 4.	
Thais size (average).....	2.6 2.5 2.6 2.7 Ave.	2.6 2.5 2.6 2.7 Ave.	2.6 2.5 2.6 2.7 Ave.	
Feeding rate, number.....	0.8 0.9 0.4 1.1 0.8	0.4 0.4 0.2 0.4 0.37	0.2 0.9 0.1 0.4 0.44	
Feeding rate, rel. vol.....	1.9 3.8 2.6 1.4 2.4	0.6 1.6 0.7 0.5 0.80	0.4 2.1 0.7 0.6 0.90	
Experiment 5.				July 1-Aug. 16, '58
Thais size.....				2.6 2.5 2.4 1.7 1.6 Ave.
Feeding rate, number.....				1.8 2.3 2.2 1.5 1.6 1.9
Feeding rate, rel. vol.....				4.0 5.1 5.0 3.3 3.5 4.7

NOTE: In Experiment 4, Cage 1 had four *Thais* in, while the other three cages had two *Thais* each. Cage 4 had only first year barnacles inside, while the other cages had three-year groups of barnacles. In all the other experiments there was only one *Thais* per cage.

only first-year barnacles as prey while the other four cages contained three year-groups.

Experiment 5—July 1 to August 16, 1958. Six cages were attached at the middle level, Area 1, at the same level as Experiment 3. A single *Thais* was placed in each of five cages, the sixth being left empty as a control. Two of the *Thais* were small, the others being average-sized (see Table 18). The barnacles were predominately one year of age.

Since two or three year-groups of barnacles of correspondingly different sizes were present in experiments 3 and 4, to compare the amounts eaten it was necessary to make an estimate of the volume of the barnacles consumed. This was calculated using the cube of the length, which is proportional to the volume. From photographs of experiments 3 and 4, the average basal length of barnacles of each age group was measured. For barnacles six months of age (in the autumn) this was 3.0 mm. The cube of the average length of each year group was expressed as a multiple of that of the six-month size. In addition, the ratios of cubes of length of *Balanus balanoides* at six months to those at 12, 18, 24 and 30 months of age, were calculated from the growth studies of Moore (1934), Hatton (1938), Barnes & Powell (1953) and Bousfield (1955); the ratios agreed well with those taken from the photographs in the present study, even though the absolute sizes differed. The calculated numbers of each age-group consumed on each area were multiplied by their respective relative volume and were then summed for all the groups.

The results of all the feeding experiments are given in Table 18. The average number of barnacles eaten in the autumn was about the same in experiments 3 and 4, but the volume consumed was greater in 4, owing to the larger size of the barnacles present. In experiment 4, a comparison of cage 4, which contained only barnacles of the most recent year group, with the other cages, reveals an interesting situation. The whelks in this particular experiment appeared to be able to open only about 1.1 barnacles per day in the autumn, fewer in the other seasons, regardless of the size of the barnacles. The whelks in cage 4 were consuming about two-thirds the volume of barnacles of the whelks in the other cages. Assuming that a greater volume means a greater amount of food, the whelks in cage 4 would be expected to have opened more barnacles if they could. There was never a shortage of barnacles in any cage. The implications of this finding are that it takes about the same amount of time for a whelk to open any barnacle, and that therefore it would obviously be advantageous for the whelk to select larger barnacles. Later in this paper evidence will be presented to show that *Thais* does select larger barnacles. The evidence that whelks can only open a limited number of barnacles cannot as yet be regarded as conclusive. In experiments 2 and 3 during the autumn, and in the other seasons the rates were higher. Also, the whelks in cage 4 may have

been exceptionally slow feeders; additional experiments are required.

Imprisonment of whelks in cages might have resulted in abnormal feeding rates, though no evidence for this could be obtained. The whelks which were marked individually (Table 17) showed an average movement of about 10 cm per tide. The dimensions of the cages in the enclosure experiments were about 12 x 12 cm, so that an average whelk may not have been much restricted in its movements by being enclosed. Although these whelks could not retreat to a refuge to rest, the corner of a cage might be regarded as a protected place. However, individual variation might have been enough to produce the differences found between the cages in experiment 4.

The feeding of *Thais* was not continuous. In order to ascertain the proportion of time which *Thais* spent feeding, the records of the whelks which had been marked were analyzed. The total population of marked whelks present at any one observation was

TABLE 19. The fraction of the population of *Thais lapillus* which was observed to be feeding at any one time. (See text for explanation.)

	No. of <i>Thais</i> marked	No. of Low Tide Obser- vations	Average Fraction of the Popula- tion Feeding at One Time	Range of Fractions Calculated from Daily Observations
Area 3, Series B				
July 18-30, 1953....	19	14	0.61	.38 - .81
Area 3, Series C				
July 18-30, 1953....	82	14	0.55	.24 - .72
Area 1,				
July 18-30, 1953....	9	9	0.64	.50 - .78
Area 1,				
Dec. 7-16, 1953.....	11	8	0.73	.43 - 1.00
Area 1, Apr. 28- May 16, 1955.....	10	11	0.49	.12 - .90

taken to be the number observed feeding on the open rock plus those which, though not visible at the time, reappeared at a later observation during this period. The results of the calculations are shown in Table 19. In the summer the population was feeding about 60% of the time, in December somewhat more, in May, less.

Another analysis was made of observations taken over twelve consecutive low tides in the summer to discover the average lengths of the feeding and "resting" periods. A summary of these observations of 79 marked individuals is given in Table 20. It was found that in the summer the whelks only fed for about half the time. Most of the periods of feeding and of "resting" were short; 70% of them were of only one or two tides duration. A few whelks fed for relatively longer periods.

In contrast to the observations on 82 marked *Thais* made in the summer, the data for the other seasons shown in Table 19 are relatively sparse. Therefore, another estimate of the proportion of time spent feeding was made. In discussing the differences in

TABLE 20. Frequency distribution of, (a.) the number of consecutive low tide periods when marked individuals of *Thais lapillus* were observed feeding, and (b.) the length of the interval between feedings. These observations were made during twelve consecutive low tide periods, of 79 marked whelks, series C, on Area 3, 0.9 feet below MTL. July 27-Aug. 2, 1953.

No. of consecutive tides	a. OBSERVED FEEDING ACTIVELY		b. INTERVALS BETWEEN SUCCESSIVE PERIODS OF FEEDING	
	No. of Observations	% of total no.	No. of Observations	% of total no.
1.....	103	60.0	74	57.4
2.....	28	16.3	19	14.7
3.....	21	12.2	11	8.5
4.....	5	2.9	9	7.0
5.....	4	2.3	6	4.7
6.....	7	4.1	6	4.7
7.....	0	0	1	0.8
8.....	2	1.2	1	0.8
9.....	0	0	2	1.5
10.....	0	0	0	0
11.....	1	0.6	0	0
12.....	1	0.6	0	0
Total:.....	172	100	129	100
Average number of consecutive tides:.....	2.0		2.2	

numbers of *Thais* observed it was shown that annual variations were small except in spring, 1954, when barnacles were absent at low shore levels and the *Thais* were concentrated at higher levels. In addition, neither the natality nor the mortality rates seemed to vary seasonally so that the seasonal differences in numbers probably reflected changes in the proportion of time spent feeding. Using the relative numbers observed in each season, and taking the proportion of time spent feeding in the summer as a base, the proportions in the other seasons were calculated (Table 21). The averages of the numbers observed in each season for two years were used to compensate for the annual variation, which was slight except for the spring. The estimates for the autumn and spring are lower than those shown in Table 19; the possibility of error in these latter estimates is great, however, since the number of marked *Thais* observed was very small. Therefore, it was decided to use the estimates from Table 21 for the later calculations of the proportion of barnacle mortality due to *Thais* predation.

Hanks (1957) has shown that a related whelk, *Urosalpinx cinerea* (Say), consumed clams at a lower rate at lower temperatures in the laboratory. It is not possible to determine from the data given whether the lower rates were due to less frequent periods of feeding or to slower activity while feeding. The low *Thais* feeding rate in spring was probably due to fewer feeding excursions rather than to a slower rate of opening barnacles. This is the spawning season,

TABLE 21. Proportion of time spent feeding by an average *Thais lapillus* in various seasons, based on the densities on Area 1, and the proportion of time spent feeding in the summer given in Table 19.

	July- Sept.	Oct.- Dec.	Jan.- March	Apr.- June
Population density (no./m ²)				
1953-54.....	66	51	13	49
1954-55.....	60	45	15	21
Average.....	63	48	14	35
Ratio to July-Sept. value..	1.0	0.76	0.22	0.51
% of time spent feeding...	60	46	13	30
1949-53 Mean Sea Temperature, °C.....	13.35	10.53	7.19	9.41

and Thorson (1958) has brought together evidence to show that many marine predators do not feed during the period when the gonads are swollen with egg or sperm. In *Thais lapillus* the present study indicates that the feeding rate was reduced at this time, although there is a possibility that feeding may have been stopped entirely for shorter periods.

EFFECT OF PREDATION BY *Thais* ON THE *Balanus* POPULATION.

As described earlier, cages were attached at three levels on Area 1 to exclude *Thais*. Some of these are shown in Figure 15. Occasionally, small *Thais*, 1/2 to 1 cm in length, entered the cages through gaps at the line of juncture of netting and rock surface. These gaps were probably caused by distortion of the cage in strong wave action or from crumbling of the rock. Since inspections were frequent and the likelihood small of a whelk escaping back through the gap, it is believed that all these entries were noted. To estimate the extent of these lapses in predator control, each occurrence was multiplied by half the time

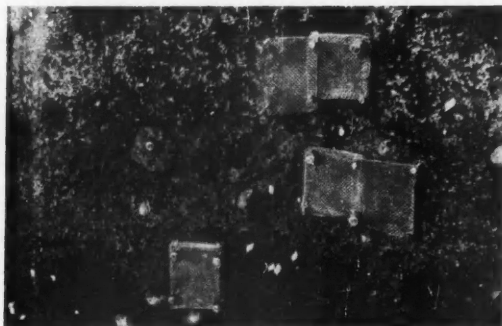


FIG. 15. Photograph of Area 1 made on April 6, 1954. The original cages and "covers" at the three levels are shown; stone 7 is attached to the left at the middle level. A true horizontal line would run slightly upward to the left, passing through both the center of the middle cage and stone 7. The dimensions of the area in the photograph are 1.1 x 0.7 meters.

since the last inspection. Summing these average times for all occurrences and dividing by the total time of attachment of the cages yields the value of 2.6% as the proportion of time when predation by small whelks occurred inside the cages. Since the cages gave complete protection against *Thais* of medium and large size, the method can probably be

sometimes bridging the spaces between the older individuals. Examples of this are illustrated in the series of photographs in Figure 19. These populations resembled the clusters of sublittoral barnacles such as *Balanus balanus* (L.) where three-year-groups were found attached to one older barnacle (Barnes 1953b). This condition did not exist on unprotected areas of *Balanus balanoides* even above the range of *Thais* predation probably because the uppermost barnacles would be very vulnerable to damage from wave-borne objects.

Since this situation was so different after a year's time from the normal one outside the cages, new caged squares were established at intervals, beginning a year after the first cages had been attached as indicated in Table 1. These resembled the natural areas closely for at least a year or more following their enclosure. With frequent visits and the addition of new cages at about yearly intervals, this method of predator control was very satisfactory. Some algal fouling on the cages occurred, especially by *Porphyra umbilicalis* J. G. Agardh; it was easily removed and constituted no problem. This fouling was much heavier on other cages attached below MTL. Limpets were placed inside the cages in the summer of 1953 to control the growth of algae which had begun to grow abundantly in the cages.

Figs. 16, 17 and 18 show the survival of barnacles on all the squares at each of the three levels of Area

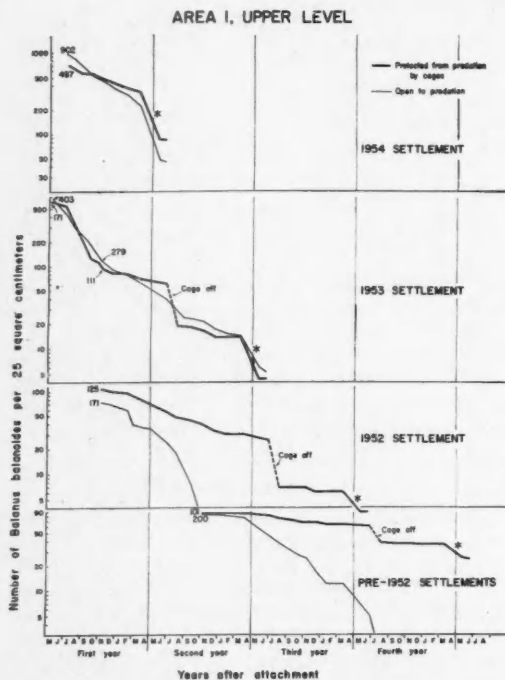


FIG. 16. Survival curves for *Balanus balanoides* with and without predation on Area 1, Upper level. The period of twelve days in July, 1954, when the cage was missing, is shown as a dashed line. The asterisk refers to the period in the spring of 1955 when the level was exposed to air for several days in warm calm weather. The initial number of barnacles counted is given with each curve.

judged effective. With infrequent inspections, modifications would be necessary. Very small *Thais*, able to pass directly through the 1/8-in mesh, were not recorded on Area 1, although their abundance low on the shore rendered ineffective there all attempts at control by cages. Only one instance of human interference occurred, in July, 1954, when the Upper Cage 1 was removed in the author's absence. A new cage was attached after twelve days of predation; the effect can be seen in Figure 16.

Besides excluding the whelks the cages gave protection from damage by water-borne objects. This protection completely altered the appearance of the barnacle population. In the two cages which were in place for 2½ years, barnacles of succeeding settlements attached to surviving adults and grew higher,

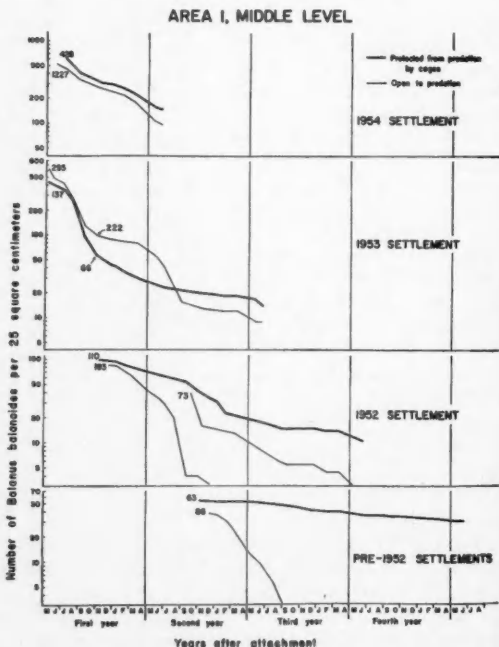


FIG. 17. Survival curves for *Balanus balanoides* with and without predation on Area 1, Middle level. The initial number of barnacles counted is given with each curve.

AREA I, LOWER LEVEL

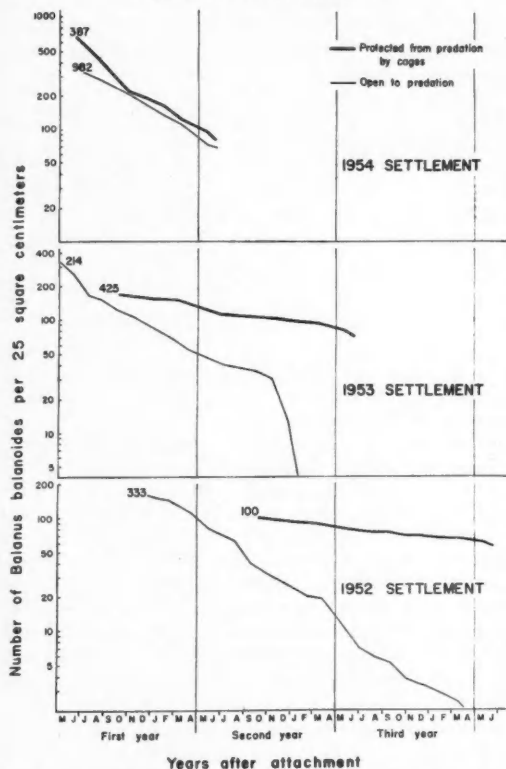


FIG. 18. Survival curves for *Balanus balanoides* with and without predation on Area 1, Lower level. The initial number of barnacles counted is given with each curve.

1. The density is indicated by the height of the curve, the relative death rate at any time by the slope. At the end of the 1953 settlement season the density of the newly settled barnacles was high at the upper and middle levels. At this time the first counts of the new set were made on smaller areas, 1.5 to 4.0 cm², within the original area. After six months the numbers had declined, and the counts of the young barnacles were made over the whole of the original area. For each such area, the end of the survival curve of the barnacles on the small area during the first six months was joined to the beginning of the curve of those on the larger, original area. The height of the curve was determined by the density of the later count made over the original area. Thus for the 1953 year group, at the upper and middle levels, the survival curves are composite ones. All others given in this paper were for the same group followed from beginning to end. The actual initial numbers are given with each curve, including those made at age six months as explained above.

Since each curve is the record of the survival of a

group of animals rather than of samples from a population, the curve must pass through each point exactly. Since no attempt was made to smooth the curves, they appear quite angular in Figs. 16-18. Some of the changes in slope were probably even more abrupt in actual fact, since some factors such as wave damage or hot weather probably operate over very short periods.

The relation of mortality to density in the early growing stages has already been discussed. A comparison of the slopes of the survival curves of caged and uncaged populations indicates that predation was a minor factor in causing the mortality during the first year above MTL; this was also illustrated in Fig. 11. The slopes of the curves first began to diverge at the end of the first year; the unprotected populations then experienced an increase in relative death rate, while that of the protected ones either remained constant or decreased. The highest death rate due to predation, (indicated by the greatest differences in slopes of the two types of curves), occurred in the summer.

The variation in age structure of the *Balanus balanoides* population at different shore levels on the area studied was similar to that described by Moore (1934) for the Isle of Man. At the top level of Area 1, near HWN, the population consisted mainly of large older *Balanus balanoides* mingled with *Chthamalus stellatus*. Below HWN, the proportion of the older age groups of *Balanus* dwindled, until near LWN only the most recent year class was present except for a short period in the spring when the survivors of the previous year were mixed with the newly settled group. Fig. 9 illustrates the survival on Area 3, below MTL.

To test whether the mortality of barnacles at low shore levels was correlated with the abundance of *Thais*, data from Area 3 were analyzed. On four portions of this area the 1954 settlement was light, so that intraspecific crowding was probably not an important cause of barnacle mortality. For seven periods between June, 1954 and May, 1955 data on both barnacle mortality and *Thais* density were available. Correlations were tested using the Spearman rank correlation coefficient (Siegel 1956) as shown in Table 22; significantly positive correlations were found in two of the four areas. In all four areas, when the barnacle mortality was high, appreciable numbers of *Thais* were present. Although the analysis is based on few observations, it suggests that in the absence of crowding at low shore levels, predation is an important cause of mortality.

On Area 1, it was seen that the death rates for the first year of life were not related to predation. Lower on the shore, where growth was much more rapid and the new set constituted the main proportion of the barnacle population, predation began much sooner. In 1954, Boulders 1, 2, and 5 of Area 3 were bare before settlement so that a completely new set occurred at this low level. *Thais* were first observed on these boulders after July 10 when the barnacles

TABLE 22. Correlation between the percentage mortality of *Balanus balanoides* and the population density of *Thais lapillus* on Area 3.

Interval	No. of Thais Censuses	BOULDER 1		BOULDER 2		BOULDER 6a		BOULDER 6b	
		<i>Balanus</i> % mort./ month	<i>Thais</i> no./m ²	<i>Balanus</i> % mort./ month	<i>Thais</i> no./m ²	<i>Balanus</i> % mort./ month	<i>Thais</i> no./m ²	<i>Balanus</i> % mort./ month	<i>Thais</i> no./m ²
June 9-July 9, 1954.....	1	2	9	7	3	5	5	1	5
July 10-Aug. 24, 1954.....	4	10	89	12	93	13	1	6	1
Aug. 25-Oct. 1, 1954.....	0	9	—	13	—	15	—	7	—
Oct. 2-Nov. 5, 1954.....	7	27	162	16	66	62	221	70	221
Nov. 6-Dec. 13, 1954.....	2	19	74	13	61	21	9	1	9
Dec. 14, 1954-Feb. 3, 1955.....	2	7	12	24	11	14	3	4	4
Feb. 4-March 16, 1955.....	7	5	28	51	78	11	6	4	4
March 17-May 17, 1955.....	16	36	77	32	45	31	12	12	12
Spearman Coeff. r_s786		.241		.714		.471	
P.....		<.05		>.05		.05		>.05	

were about 8 weeks of age. In 1955, boulders at various levels were scraped clean a month before settlement. These received their first settlers at the beginning of April; whelks were first observed feeding on the lower of these areas, adjacent to Area 3, on May 11, when the barnacles were only 5 to 6 weeks old. On similarly treated areas above MTL no feeding by *Thais* occurred.

The difference between the two years, 1954 and 1955, in the age at which predation began may possibly be explained by the differences in distribution of *Thais*. In Fig. 13 it is shown that many fewer *Thais* were present on Boulders 1 and 2 in May and June of 1954 than in these months in 1955. Also, there were adult barnacles present on these areas in 1955 but not in 1954 (Fig. 9). It appears that the presence of adult barnacles attracted large numbers of *Thais*, which then began to feed on the newly settled barnacles, even on adjacent areas from which all adults had been removed. In the following discussion it will be demonstrated that *Thais* does tend to feed more on adult barnacles so that the presence of adults would be expected to attract more *Thais*. Fischer-Piette (1935) noted that *Thais* did not attack *Balanus balanoides* until six months after attachment; no indication of shore level was given, however.

If, whenever it is "hungry," a *Thais* feeds on the barnacles it is then touching, it would be expected to encounter and feed on the various age groups in direct proportion to the area covered by each. From this hypothesis, some feeding would have been expected to occur on the newly settled group on Area 1. Since this did not happen to any extent, it must be concluded that the whelks ignored this young group and selected older individuals. These older barnacles, besides being larger, had rough shells, the upper edges of the wall and opercular plates being worn and rounded. This may have enabled *Thais* to distinguish older individuals.

Besides this evidence of selection some direct observations were made in a simpler situation where only

two age groups were present. In May, 1955, some *Thais* were noticed feeding between MTL and LWN on the new set when it was 5-6 weeks old. Some were feeding also on survivors of the previous year, although these comprised only a small proportion of the total barnacle cover. The *Thais* thus had two groups of contrasting sizes to choose between. The proportions of the area occupied by old and young barnacles were determined by laying a meter square frame divided into 100 cm² squares on the rock, and for each small square separately, estimating by eye the total barnacle cover, the coverage of the older group (their yellow shells contrasted well with the white shells of the young barnacles) and the percentage of these older barnacles which were alive. By estimating each small square independently it was believed that a very close approximation to the true proportions was made. On each rock area, one horizontal and two vertical transects were made of ten such squares. Since at this stage very few young were dead, the coverage of living young ones was calculated as the total barnacle cover minus the coverage of older barnacles. This estimate of older barnacles included both dead and live individuals, so that it was multiplied by the percentage alive to give the area of living older individuals. The proportion of live old to live young was then calculated. Since some young which had settled inside the dead adult shells were missed and some adults killed by *Thais* still had their opercular plates in place, it was believed that the error in the measurement tended to overestimate the proportion of living adults.

On the assumption that no selection between the two groups by *Thais* was taking place, it would be expected that the *Thais* actually observed feeding would be distributed at random over the barnacles. In other words it would be expected that there would be a direct relationship between the numbers of *Thais* feeding on each age group and the areas covered by each group. To test this hypothesis, on these areas each *Thais* was carefully tilted away from the surface to expose the individual barnacle upon which it was

TABLE 23. The numbers of *Thais* observed to be feeding on two age groups of *Balanus*, compared to those numbers which would be expected if *Thais* occurred on each age group of barnacles in proportion to the area covered by it.

	OBSERVED AND EXPECTED NUMBERS OF <i>Thais</i> FOR EACH DAILY OBSERVATION.												TOTAL NUMBERS	
	May 18 Obs. Exp.	May 18 Obs. Exp.	May 19 Obs. Exp.	May 19 Obs. Exp.	May 20 Obs. Exp.	May 20 Obs. Exp.	May 21 Obs. Exp.	May 21 Obs. Exp.	May 22 Obs. Exp.	May 22 Obs. Exp.	May 24 Obs. Exp.	May 24 Obs. Exp.	Obs. Exp.	Obs. Exp.
No. of <i>Thais</i> feeding on one year old barnacles:	49	12	28	8	25	6	30	7	36	9	28	8	196	50
No. of <i>Thais</i> feeding on newly settled barnacles:	10	47	11	31	6	25	8	31	9	36	11	31	55	201
Total <i>Thais</i> Observed:.....	59		39		31		38		45		39		251	
Chi-square (1 d.f.):.....	143.20		62.90		74.60		92.63		101.25		62.90		532.36	
Probability:.....	<.001		<.001		<.001		<.001		<.001		<.001		<.001	

feeding. When a *Thais* was feeding on a barnacle the opercular valves were usually opened out, with a white "cleaned" spot at the juncture of the valves. This spot appears to be made by the whelk in the process of opening the barnacle. Since it occurs in both old and new barnacles, it made the identification of the individual being eaten equally certain in both groups. In some instances the *Thais* was attached to the rock surface or to an individual barnacle which showed no sign of being attacked. These instances were noted as indeterminate, and were not used in the calculations. The results of these observations are given in Table 23. The total number of *Thais* feeding each day would be expected to be divided between the two barnacle groups in proportion to the areas occupied by them if there was no selection. Comparison of the expected and observed distributions (chi-square) showed that selection was certainly taking place; the whelks were consistently choosing the adult barnacles. The heterogeneity chi-square was 4.12, $p=0.50$, affirming this conclusion.

Some areas, adjacent to those just discussed, having been scraped clean before the 1955 settlement began, were covered only by newly settled individuals. The whelks feeding on these individuals, which were then 5 to 6 weeks old, seemed from casual observation to be eating the larger of these barnacles. To test this observation, on these areas each *Thais* was lifted as before and the individual being eaten was identified and measured. On the same day a piece of the rock was chipped off from the same area and was brought into the laboratory where all the individuals on a small area were measured to indicate the size variation in the total prey population. Measurements were made on six days. Combining all measurements, those representing the whole prey population yielded an average length of 2.0 mm, range 0.8 to 3.7 mm. Of those being eaten by *Thais*, the average length was 2.8 mm, range 1.7 to 3.8 mm. The difference between the two sets of measurements was found to be highly significant ($p = .00003$), using the Mann-Whitney U test (Siegel 1956). Since those being eaten were not apparently rougher or more eroded than the smaller individuals, size alone seems to be the stimulus to the whelk. Large bar-

nacles in a dense settlement tend to stand apart as individuals in comparison to the many average-sized individuals around them, and this may create a spatial discontinuity acting as a tactile stimulus to *Thais*. This situation is illustrated in Fig. 7.

Little information was obtained concerning the feeding rate of different sized whelks. As shown in Table 18, the whelks which were less than 1.7 cm in height in experiment 5 ate at a slower rate than did the larger ones. In the other experiments, however, where the sizes were not so different, the correlation was less clear. It is obvious that there was much individual variation among whelks of about the same size.

There was no obvious correlation between the size of the whelk and that of its prey. In the observations on size selection of barnacles 5-6 weeks old, the size of some of the whelks was measured at the same time as that of the barnacles being fed upon. The average size of the 55 whelks measured was 27.1 mm, all but nine being between 25 and 30 mm. The average length of the killed barnacles was 2.8 mm. The very large or small whelks showed no consistent relation to the size of their prey. A scatter diagram of size of whelk vs. size of the barnacle being fed upon showed no trend, but only a cluster of points near the average sizes of the two animals. The extreme individuals showed irregular behavior.

One other aspect of whelk behavior which might have a bearing on the selection of larger barnacles is the habit-forming behavior described by Fischer-Piette (1935). Fischer-Piette described how the whelks have difficulty in changing their food from barnacles to mussels. The mussels were usually drilled through but barnacles were only rarely drilled. In the present study a few barnacles were found drilled through one opercular valve or, once, through the side wall; these were in a cage below MTL in which only very small whelks were present. More usually, the opercular valves were opened in the same way as the barnacle opens its own valves, that is to say, outward. As pointed out earlier, barnacles which have been opened by *Thais* usually show a small white area at the juncture of the two opercular valves, which is formed by the

removal of the outer layer of shell so that a smooth "cleaned" spot remains.

The method of opening barnacles thus appears to be very different from the drilling of large mussels and may well require some "learning," as described by Fischer-Piette. In the present study, the only very large barnacles which were found below MTL together with dense *Thais* populations were in rock spaces kept clear by *Patella vulgata* on a reef otherwise covered with mussels. Here it might be that the whelks had formed the habit of eating mussels and so ignored the few barnacles.

It was decided to test the possibility that the choice of larger, eroded barnacles in preference to the smoother newly settled individuals was due to a habit, developed after feeding in late autumn and early spring on these older barnacles. The method of feeding was not different, as in the mussel-barnacle situation described above, but direct evidence was judged desirable. Therefore during observations in May, 1955, individuals feeding on older barnacles were marked with brown paint, and those feeding on newly settled barnacles with red. Of the 25 whelks marked as feeding on older barnacles, 1, 5, and 2 individuals were observed during the next three observations feeding on new barnacles; conversely, of the 21 whelks originally feeding on new barnacles, 5, 7, and 3 were found feeding on older barnacles in the next three observations, respectively. Thus about a quarter of the whelks changed the size of their prey over a period of three days. The preference shown for older barnacles does not appear to be due to a preformed habit.

The advantage to *Thais* of selecting large barnacles as prey is evident if it can only open a fixed number of barnacles in a given time, as the evidence from the feeding experiments indicated. Since *Thais* selects the larger barnacles, the danger from this predation increases with the age of the barnacle. Only in a narrow zone above MHWN are the barnacles free from predation by *Thais*. Thus the variation in the age structure of the *Balanus* population at different shore levels appears to result principally from the variation in distribution of *Thais*. This was shown in the caging experiments on Area 1, where the age structure of the population in the high zone above MHWN was reproduced inside cages lower down after two year's protection from *Thais* predation.

This selection by *Thais* of large sized barnacles may explain a conflict in the literature concerning the growth rate of *Balanus balanoides* at different shore levels. Moore (1935b, 1936a) collected barnacles at various localities and levels in summer, and separated them into two age groups, the current year's set, aged 2 to 3 months, and the previous years' sets of 14 months or older. Hatton (1938) followed the growth at three levels on the shore for 3 years, while Barnes & Powell (1953) measured individuals on intertidal panels attached to a pier for 1 1/2 years. The level at which the largest average size occurred at ages of 2 1/2 and 14 months respectively is given for each of these studies in Table 24; the largest barnacles in the first growing season were almost always low on the shore, but in the second season there was great variability. In the studies of Moore and Hatton, the lo-

TABLE 24. A comparison of the average sizes of *Balanus balanoides* at different intertidal levels in Great Britain and Northern France. Measurements of young and adults were made under various conditions of wave action and salinity.

Location and Authority	Collecting Stations	Environmental Conditions	SHORE LEVEL AT WHICH THE LARGEST AVERAGE SIZE WAS MEASURED		Relative abundance of <i>Thais lapillus</i> at each location
			Age 2-3 months	Age 14 months	
Plymouth, England. Moore, 1936a	Hen Point.	Brackish water	Low	Low	Absent
	Tinside, Drake Is., Misery Pt.	Normal salinity	Low or Middle	About the same at all levels	Common
Isle of Man, Irish Sea Moore, 1935b	Bradda Head	Heavy wave action	Low	Low	Few
	Dub Reef, Port St. Mary	Moderate to few waves	Low	High	Common
St. Malo, No. France Hatton, 1938	Decolte Ouest	Heavy waves	Low	Low	Few
	Decolte Est	Sheltered	Low	High	Common
	Cite	Sheltered, strong current	Low	High	Common
Millport, Scotland Barnes & Powell, 1953	Panels on Keppel Pier	Sheltered, strong current	Low	Low	Absent

NOTE: Size was expressed in tissue weight by Moore and in linear dimensions of the shell by the other authors.

cations with strongest wave action, or where the water was brackish, continued in the second season to have the largest barnacles at low levels, while in protected areas or at normal salinities, the situation was reversed. At Millport, the barnacles were always largest at low levels.

Moore thought that the growth of older barnacles might be retarded by a harmful factor in sea water, which would operate longer at low levels, but would be offset by the greater food supply in wave beaten places or in brackish estuaries where suspended matter was abundant. There is as yet no evidence for this hypothesis. Sokolova (1951) found that *Balanus balanoides* in Russia (Arctic Ocean) grew faster at low levels during their second summer.

Barnes & Powell (1953) showed that the specific growth rate was inversely proportional to the size of the barnacle. They suggested that the better growth which Moore and Hatton found at high levels in the second season resulted from the smaller barnacles growing faster because they were smaller at the

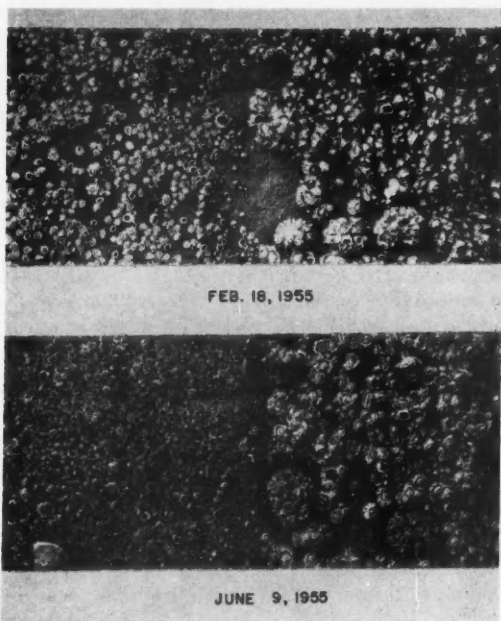
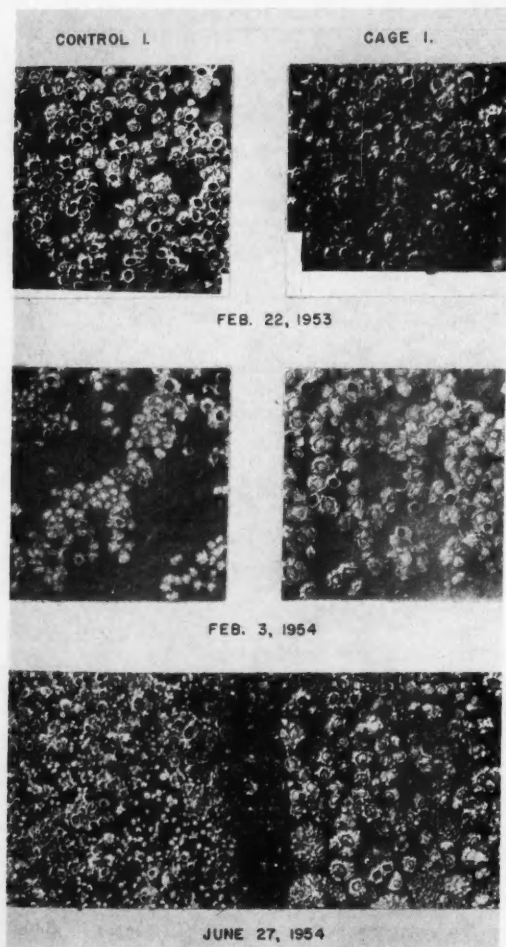


FIG. 19. The effects of protection from predation and damage for 2 1/2 years. Photographs of the Middle Control 1, left, and Middle Cage 1, right, were taken at intervals throughout the study. The dimensions of the area represented by the photographs are about 16 x 7 centimeters.

start of the second season. This is undoubtedly true, but it does not explain why the high level ones should be larger than those lower down. Although the high level barnacles studied by Barnes & Powell showed a slightly higher specific growth rate in the second season's growth, the absolute growth rates were about the same on their highest and lowest panels, nos. 3 and 7, so that the difference between the average sizes on these panels was the same at age 18 months as it was at 9 months, the barnacles at the low level still being larger.

An alternate explanation might be as follows. Predation by *Thais* tends to eliminate the larger individuals and so would reduce the mean length. Since this predation occurs much more heavily at low than at high levels, the average size at the low levels might well be found to be smaller than at higher levels in the second season. Where predation is light or absent, the effect of longer feeding time would continue to favor growth at low levels so that at the end of the second season the average size would still be larger there. The rather larger decreases in average size found by Hatton (1938) at low levels were thought by him to be due to irregularities in shape or erosion; measurements of a single barnacle made by Hatton & Fischer-Piette (1932) showed this. However, Deevey (1947) suggested in reference to the data of Hatton (1938) that there may have been a greater mortality of older

individuals from unknown causes. From the present evidence, this would appear to be the case, with predation the cause.

Moore (1935b, 1936b) observed that *Thais* was absent or less common in brackish water or in very wave beaten situations. Assuming that this was so at the three locations studied by Hatton, the relative abundance of *Thais* has been deduced and the estimates included in Table 24. The places where *Thais* was relatively more common were also those where the average size was smaller at low levels. Thus the differing results seem to have been due to variations in selective predation. When studying the growth rate of an animal it is therefore important to establish that any mortality which occurs is random with respect to size.

THE PROPORTION OF THE TOTAL MORTALITY OF *Balanus* CAUSED BY PREDATION AND OTHER FACTORS

With the data collected on the numbers and feeding rates of *Thais* over two years on Area 1, it was possible to calculate the number of barnacles which could have been eaten by the observed population of *Thais* per unit area and time. This was done for periods of three months' duration, regarding January through March as the winter season when the sea water temperature was lowest (Barnes 1955), and the other seasons accordingly.

Since the total mortality rate of the barnacles during each of these seasons was also known, the mortality which could be accounted for by predation by *Thais* was expressed as a proportion of the total rate. In addition, some mortality occurred inside the cages on Area 1, presumably from agents other than large predators or damage from floating objects. Intraspecific competition for space, disease, parasites and the effects of weather were possible causes of this mortality. This "caged" mortality rate was also expressed as a proportion of the total mortality rate occurring outside the cages. Thus the total mortality rate of *Balanus* during each season at each level was divided into three fractions: that which would have occurred even with protection by cages, that due to predation by *Thais*, and a remainder which may have been due to other predators or damage.

A correction had to be applied to the feeding rates of *Thais* given in Table 18 before they could be used in this calculation. The rates gained from *Thais* enclosed in cages included both periods of feeding and "resting." However, the *Thais* counted on the vertical surface of Area 1 were undoubtedly engaged in active feeding. For example, in the summer, the average feeding rate of *Thais* in cages was 1.9 barnacles per day. However, since *Thais* fed only about 60% of the time in summer, the rate during this active period was 3.17 per day; thus for each season the feeding rates were corrected using the proportion of time spent feeding as given in Table 21. These corrected rates are given in Table 25. As shown in this table, for both the autumn and winter, feeding rates from two separate experiments were available.

TABLE 25. Corrected feeding rates (No. of *Balanus* eaten by one *Thais* per day) at the level of Area 1. The rates from Table 18, experiments 3 to 5, are here recalculated to eliminate the periods spent "resting" between feeding excursions.

	Winter	Spring	Summer	Autumn
Average Feeding rates, from Table 18:				
Exp. 3..	0.05	1.45		0.9
Exp. 4..	0.37	0.44		0.8
Exp. 5..			1.9	
Mean of these rates:	0.21	0.44	1.9	0.85
Fraction of time spent feeding (from Table 21).	0.13	0.30	0.60	0.46
Feeding rate (per day) during the period of active feeding.....	1.62	1.47	3.17	1.85
Same rate per 90 days.....	145.	132.	285.	166.

For the summer, the rate from experiment 1, lower on the shore, was very close to that of experiment 5. Only one estimate is available for the spring, from experiment 4. The average of this rate with that of the summer from experiment 5 is 1.17; this average shows fair agreement with that of 1.45 over the spring and summer from experiment 3.

In making the calculation, the number of barnacles which could have been eaten by *Thais* was subtracted first from the total number which had died. Then the number which would have died even if the area had been protected by cages (calculated from the relative mortality of those in cages) was subtracted, leaving (sometimes) a remainder. Some of the barnacles which supposedly died from causes included under "caged" mortality might have been killed by the various deleterious factors, such as predation and damage, which operated only outside the cages. A correction was made for this, thereby increasing the proportion of the total mortality due to factors occurring outside the cages.

There are several possible sources of error in these calculations. Individual variations occurred in the feeding rates of *Thais*, as shown in Table 18. It is felt, however, that these were not extreme, and were probably not biased in one direction. All sizes of *Thais* which occurred in any abundance on Area 1 were used in the feeding experiments, and two independent estimates were available for each season except spring. The most divergent estimates were those in the winter. The proportion of time which *Thais* spent in feeding in the summer was estimated in two independent ways (Tables 19 and 20). The extension to the other seasons (Table 21) may have introduced some error, since the calculation was based on the assumption that seasonal differences in abun-

dance were the result of differences in the frequency of feeding rather than of mortality. The estimates of population density of those *Thais* which were seen feeding in different seasons were based on many censuses, but these were not made with equal frequency in all seasons. In addition, the fact that *Thais* sometime occurred in groups rather than being distributed at random would reduce the accuracy of the censuses.

From all these considerations, it appears that the information about *Thais* is most accurate for the summer, and somewhat less so in the autumn. In the spring only one separate feeding rate is available, but as discussed previously, it is probably not greatly in error. The winter rates were quite different in the two experiments, but errors in this season were rendered less important since the numbers of *Thais* which were active at this season were small (Fig. 14) and so contributed little to the mortality of the barnacles.

By comparison, the estimates of the mortality of the barnacles were much more accurate. For the uncaged areas there were at least two replicates at each level. For the first year there was only one cage at each level; in later years more cages were added. The data from areas caged for more than about one year were not used, since the age structure of these populations had become very different after being protected for this length of time. The only exception to this procedure was at the lower level, where only one cage was present; the barnacles became densely crowded after the autumn of 1954. This is probably the only instance where the caged population is not representative of the natural population. In the rest of the estimates, the total mortality and the portion representing "caged" mortality are probably accurate ones, while the fraction representing mortality from *Thais* is a less accurate estimate. Only those barnacles aged 6 months and older were included in these calculations. As shown in Figs. 16-18, barnacles less than 6 months old were not fed upon by *Thais* on Area 1.

As shown in Fig. 20, the effect of *Thais* was greatest in the summer. At every level in both summers (except at the lower level in 1953), *Thais* could have accounted for all the mortality of *Balanus balanoides*. In some other seasons, especially when the amount of "caged" mortality was high, *Thais* also accounted for most of the remaining mortality. There was a "remainder," unaccounted for by *Thais*, in 5 of the 6 winter periods at all levels, and in certain of the other cooler seasons. This may perhaps be attributed to damage during severe gales.

The proportions given in Fig. 20 included all barnacles older than six months. If those aged between 6 and 18 months were considered separately from the older ones, differences in the proportions were found. As was shown in the survival curves of Figs. 16-18, the mortality inside the cages was very low after the age of 18 months. In these older barnacles the only seasons when the "caged" relative mor-

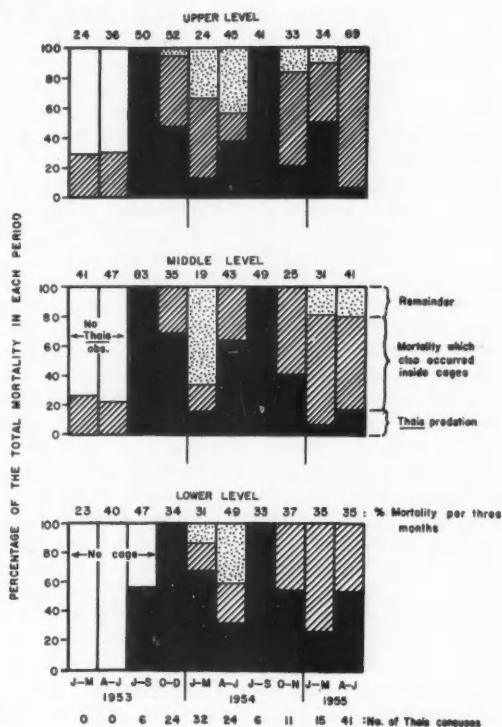


Fig. 20. Proportions of the total mortality of *Balanus balanoides*, over 6 months old, in each season on Area 1, which could be ascribed either to predation by *Thais lapillus* or to factors which operated inside the cages. See text for further explanation.

tality rate exceeded 12% were the autumn of 1953 and the spring of 1955; mortality during the latter period has already been discussed. In contrast, the "caged" relative mortality rate of the younger group was generally high, the average mortality rate per season in the cages being 23.5% for the young group as compared to 9.8% for the older group.

With regard to predation, the evidence that *Thais* selects larger barnacles as prey was used as follows. It was assumed that *Thais* attacked members of the older group first. For each season and level the number of barnacles calculated as having been eaten by *Thais* was compared to the number of the older group dead in excess of "caged" mortality. In all instances the former number was greater; in other words, *Thais* could have accounted for all the mortality of older barnacles in excess of the "caged" mortality. It is improbable that *Thais* accounted for every such death, but when it is considered that older barnacles with heavier shells are much less likely to be damaged by objects thrown about by waves, the likelihood is high that *Thais* is the main cause of death in older barnacles below MHWN level.

As discussed earlier, in the summer of 1958 the population density of *Patella vulgata* was much lower

than it had been in 1955, and the cover of *Fucus* was greatly increased. The age structure of the *Balanus balanoides* population was much different also. The mean densities (no./100 cm²) on Area 1 in July, 1958, for the 1958, 1957, and 1956 year groups were, respectively, 74, 270 and 2; obviously the 1958 settlement had been very light. The high proportion of the 1957 year group, (then just over one year old), to the older groups was also unusual. In the summers of 1953, 1954 and 1955, the densities of one year/older year groups were respectively, 223/77, 157/17 and 300/26, with an average of 228/40. Thus the value of 270/2 in the summer of 1958 shows a much lower proportion of barnacles aged two years or more. This low value for the older barnacles was not due to poor settlements, since the 1955 and 1956 settlements on other areas were good (Table 9). Hummocking was never seen on Area 1, so that the low density of these age groups was probably not due to intense intraspecific crowding. From the previous evidence that *Thais* selected larger barnacles it was natural to ascribe the low proportion of older barnacles to increased predation by *Thais*. The average densities of *Thais* on the same three levels of Area 1 in which the densities of *Balanus* were calculated, for the summers of 1953-1955 were 12, 14 and 4 per 0.2 m², respectively; for the summer of 1958 it was 16. The slightly higher density of *Thais* in 1958 may be indicative of greater predation, but no direct evidence is available on densities of *Thais* earlier in the year, when the mortality of the older barnacles must have occurred. Some indirect evidence exists, however, which suggests that the *Thais* population may have been higher on Area 1 since the previous winter.

In the censuses of *Thais* made in the summer of 1958 it was noticed that many *Thais* occurred on the barnacles beneath the cover of *Fucus*. To test whether the *Thais* tended to occur more densely under the *Fucus* canopy than in the open, the total number at each level in ten observations was divided into the proportions in which the surface was covered by *Fucus* or bare. These are the numbers which would be expected if the distribution of *Thais* bore no relationship to that of *Fucus*. These numbers were compared (chi-square) to those observed under the *Fucus* canopy and in the open. At every level more *Thais* were observed to be under the algae than would be expected in a random distribution. The total chi-square probability was less than 0.0005; the *Thais* evidently tended to occur more densely under *Fucus*. Most of the smaller *Thais* found on Area 1 in the summer of 1958 were under the *Fucus* canopy. Moore (1938b) found very young *Thais* only near the bottom of the shore; evidently young *Thais* are less tolerant of dry conditions. An increased coverage of *Fucus*, such as had occurred on Area 1 since the summer of 1957, would thus render the area more favorable for younger *Thais*, so increasing the total numbers of *Thais*. If this occurred, heavier predation on the older groups of *Balanus* would be expected to follow,

with the resultant effects on the age structure of the *Balanus* population seen in the summer of 1958.

DISCUSSION AND CONCLUSIONS

While the various environmental factors measured in this study have been shown to cause much mortality, other "intrinsic" causes may have been important. Pearl & Miner (1935) cite the rate of living and genetic constitution as the two main endogenous causes of death. Neither from the present study nor from previous work on this species has any information been found concerning genetic factors. With regard to the rate of living, relative growth was found to be faster at low levels in the first year, at high levels later (Barnes & Powell 1953). Rate of activity, as represented by cirral beat, was studied by Southward (1955), for barnacles from different shore levels. *Balanus balanoides* gave ambiguous results; the cirral beat was faster in those from low levels soon after collection, but the differences disappeared after a short time in the laboratory. In any case, cirral beat may not be a good measure of activity in natural conditions. Observations were made at Millport of *Balanus balanoides* just after the rising tide had covered them on a calm day. They extended their cirri stiffly facing the current, retracting after irregular intervals of up to twelve seconds, presumably after having caught a particle of food. Similar behavior under natural conditions has been described in *Chthamalus stellatus* (Crisp 1950). Segal, Rao & Thompson (1953) found that limpets and mussels taken from lower levels had faster heart beat and water propulsion, respectively, even after acclimation in the laboratory. Acclimation was achieved within a month when limpets were transplanted in the field. It is obvious that, as yet, the extrinsic and intrinsic causes of mortality in barnacles cannot be separated.

As a means of summarizing the changes in population density which occurred at various levels during this study, the cumulative curves of Figure 21 have been plotted. Three locations were selected to illustrate the differences between shore levels, these being the top and middle levels of Area 1 (both caged and uncaged areas at the middle level), and two boulders from Area 3. These represented the upper and lower limits of distribution (except for scattered individuals) of *Balanus balanoides*, together with a mid shore level where successful predator control had been exercised for the entire period of study.

Fig. 21 illustrates several points dealt with previously. Barnacles live shorter lives at the lower levels, never more than two year-groups being present together. At the top levels, early mortality may result in only a few barnacles surviving after a year, but these may then live for a long time. The "dominance" of the 1952 year-group is shown.

At the middle level, the survival of older barnacles protected from predation was almost equal to that at the higher levels, but the early survival was better, probably owing to the less extreme physical conditions. This resulted in more equal representation of

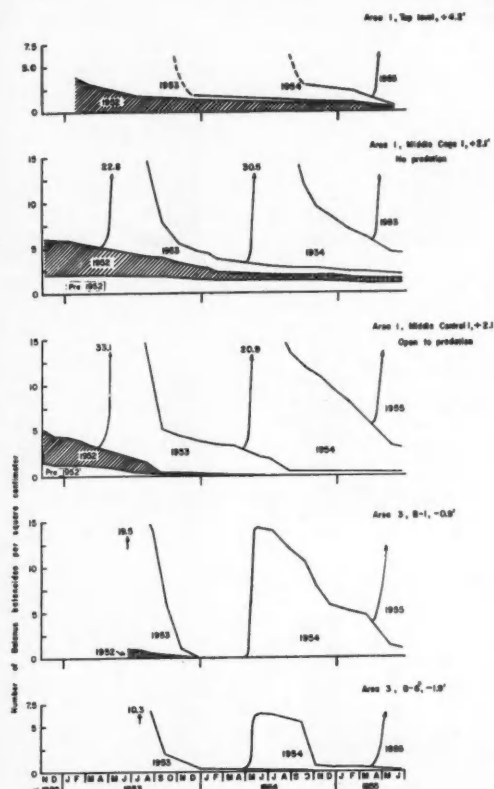


FIG. 21. Cumulative curves of the numbers of *Balanus balanoides* present at various shore levels; the height of each level is given, in feet above or below MTL. The upper portion of the curves just after settlement have been omitted in some cases; the densities reached have been indicated. For comparison, the 1952 settlement has been shaded in all instances.

each age group as compared with the higher levels. On the natural area unprotected from predation there were usually two year groups present, three at times, in contrast to the low levels.

In comparing the caged and uncaged areas at the middle level of Area 1, it is apparent that there was not much difference in the numbers of barnacles present, although the age structure of the population was very different. However, the older barnacles, being larger, occupied more surface space and represented a greater biomass per unit area owing to their greater height. To illustrate this quantitatively, measurements were made from a photograph (shown in Fig. 19), of these two areas made February 18, 1955, after the barnacles in Middle Cage 1 had been protected for 2 1/4 years. Surface areas covered by each age group were measured with a planimeter. As a relative measure of volume, the surface area of each age group was multiplied by the average height of the same group. This average height was deter-

mined by first obtaining the average length of the age group from the photograph. Then measurements of length and height of a group of *Balanus balanoides* collected from Area 1 in August, 1958, were made. From these data, an average height was determined for each age group, using the average length obtained from the photograph.

This calculation of volume can be used to compare different age groups only if the barnacles do not change shape as they grow. In the measurements made by Barnes & Powell (1953) of barnacles growing without crowding on panels, the barnacles became squatter as they grew, average length/height ratios of 2.4 and 3.3 being found at average lengths of 3.1 and 6.0 mm, respectively. In the present measurements of barnacles collected from Area 1, the barnacles changed shape only slightly: average length/height ratios of 1.7 and 1.6 were found with average lengths of 2.6 and 6.6, respectively. This difference in the reverse direction was probably the result of moderate crowding on Area 1. Since the barnacles change shape only slightly under these conditions, a valid comparison may be made between the calculated volumes of the different age groups.

The comparative measurements of number, surface area and relative volume for the different age groups with and without predation are given in Fig. 22. Without predation a greater volume (standing crop biomass) was supported by the same area while providing less bare rock surface for settlement of the new age group later in the spring (although some settlement may occur on the shells of the older barnacles). Since the number of larvae produced is proportional to the volume (Moore 1935a, Barnes 1953a), the effect of predation was to reduce greatly the larval output as well as the standing crop. Since there was usually a great oversupply of larvae seeking places to settle, the predation probably was not enough to limit recruitment. But by providing more space for new settlement and removing the older barnacles that grew more slowly, predation by *Thais* may have increased the rate of production of biomass. Therefore the predators, by selecting the larger barnacles, may have evolved a method of harvesting tending toward the "optimum yield." This provides an example from a natural population paralleling that of the artificial predation on fish by fishermen using nets which select the larger sizes. Fishermen, of course, strive for an optimum yield, with varying success.

In discussing the mortality at high shore levels, it was shown that annual variations in the mortality and strength of successive year classes were greater there than at lower levels. As can be seen in Fig. 21 more extreme variations occur at low than at middle levels. At the higher level the fluctuations were undoubtedly due to chance occurrence in the weather, such as occurred in the spring of 1955, although even less extreme conditions could probably cause destruction in young barnacles. At the low levels, overpopulation led to the formation of unstable "hum-

mocks" since growth was faster at these levels. In addition, the numbers of *Thais* showed greater fluctuations at low than at mid shore levels, as shown in comparing areas 3 and 1, Fig. 13. Thus fluctuations in the physical factors decrease toward lower levels while variations in the biotic factors, such as crowding and predation, decrease at higher levels. Since mortality at high levels is due mostly to physical factors (there being little evidence of predation from the land, by mammals, birds, etc.), while mortality at low levels is mainly due to biotic factors, the damping of the fluctuations in both these as mid shore levels are approached tends to result in less variability in the mortality here. The intertidal zone of *Balanus balanoides* is thus bounded by physical factors at the top and biotic ones at the bottom, with fluctuations in mortality caused by these factors being greatest at the limits and decreasing toward the mid tide region.

SUMMARY

The accessibility and sessile nature of intertidal barnacles allowed very accurate records to be made on recruitment and survival under natural conditions.

Recruitment occurs as settlement after a planktonic larval period. The population density of *Balanus balanoides* after settlement was determined by the space available and the mortality during or just after settlement, rather than by a limited supply of larvae from the plankton, in most of the years studied. Attached larvae were killed during warm weather, but once metamorphosed, most early mortality was a result of damage from wave-borne material. Those young barnacles in hollows suffered least, so that the settlement density on a surface was partly a function of the proportion of protected sites. Larvae were liberated by adults into the plankton at intervals. Some of the first settlers were smaller and did not survive well, while those arriving later in the season were forced to settle in less favorable sites and suffered heavier mortality. Limpets damaged newly settled barnacles, but no other animals appeared to cause mortality at this time.

When the barnacles began to grow they soon touched each other at moderate population densities. Crowding then ensued, and barnacles were killed when they were undercut and displaced, smothered, or crushed by growing neighbors. In the first growing season, mortality was greater when population density was higher. At low shore levels the relative growth rate was faster and crowding and mortality were consequently greater. Crowding also resulted in some barnacles assuming unstable growth forms. These barnacles were detached in later storms and so there was sometimes a lag in the mortality due to crowding. Growth was slower in later years, and older barnacles were affected by crowding only when young barnacles attached themselves to the older ones and smothered them. When barnacles were protected from predation in cages, the mortality de-

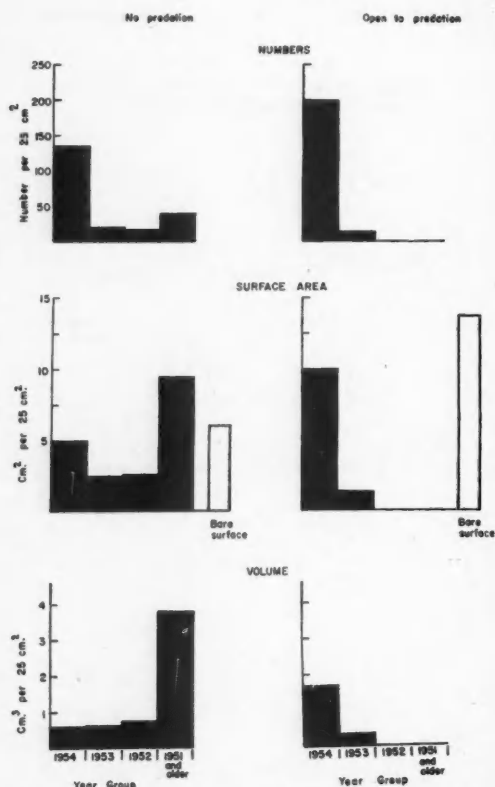


FIG. 22. A comparison of the populations of *Balanus balanoides* on two adjacent areas, Middle Cage 1, left, and Control 1, right, after the former had been protected from predation for 2 1/4 years. The data were taken from a photograph made on February 18, 1955, shown in Figure 19.

creased during the first winter and increased slightly during the next spring and summer, decreasing in the following years. This is also the pattern of growth, and indicates that intraspecific competition for space had a great effect on survival during the first year of life.

The upper shore limit of distribution was probably set by adverse weather conditions. Most of the mortality there occurred in the first year of life. Occasional periods of warm, calm weather may kill most of the younger barnacles at high levels; the erratic nature of this factor produces dominant year classes there.

The most important predator was a gastropod, *Thais lapillus*. It did not occur as high on the shore as *Balanus*, and was scarce below the lower limit of *Balanus*. It was less abundant during the winter and spring, which is its spawning season. In summer it fed about 60% of the time, and moved about 10 cm per tide, with much variation. Its feeding rate on barnacles was greatest in summer, probably due

to the greater frequency of feeding excursions at that time.

From experiments where *Thais* was excluded from small populations of *Balanus* it was discovered that *Thais* selected the larger barnacles as prey; direct observations confirmed this finding. This behavior accounts for the changes in age structure of the barnacle population at different shore levels. Above the upper limit of *Thais* distribution several year groups of barnacles occurred together. Lower on the shore the older barnacles were selected by *Thais* and the number of concurrent age groups was less there. Near the lower limit of *Balanus* distribution where fewer older barnacles occur, predation began earlier in the life of the barnacles.

Previous studies of the growth rate of *Balanus* made by measuring samples of the population resulted in erroneous conclusions, partly because the mortality at lower levels (with *Thais* predation) was not random with respect to size.

Calculations of the proportion of the total mortality caused by predation by *Thais* showed that in the summer it could account for all of the mortality of barnacles older than six months. In other seasons it was less important. Annual variations in the intensity of predation occurred.

The evidence from the measurement of feeding rate of the predators suggested that they could open only a certain number of barnacles per day, regardless of size. If so, it provides evidence for the selective advantage to *Thais* of a behavior trait for selecting larger barnacles as prey. In addition, the evolution of such a trait would tend to increase the productivity of the barnacle population, by providing proportionately greater space for new settlers which grew relatively faster. Thus this behavior tends to produce the "optimum yield" for the predator population.

The barnacle zonation on the intertidal shore seems to be bounded at the top by deleterious physical factors (weather), at the bottom by biological ones (competition for space and predation). The fluctuations in these factors were greatest at the upper and lower limits; the recruitment and mortality were less variable at the middle shore.

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